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THE SPECIES CONCEPT* THE LOGICAL BASIS OF THE SPECIES CONCEPT

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THE species concept in biology is essentially a product of eighteenth century rationalism. That great century was the epoch of Voltaire, of David Hume, of Immanuel Kant, of Thomas Jefferson, of Antoine Lavoisier. It was the period of political democracy, of the critical philosophy, the nebular hypothesis, the origin of chemistry. Man, working on the basis of two centuries of scientific achievement, set out to formulate a rational system of the world. This was the intellectual climate in which Linnaeus developed the species concept, and the species concept was biology's contribution to the rationalization of man's experience.

Two centuries before biology had risen phoenix-like from the ashes of its Greek beginnings. The animal body was carefully dissected and the circulation of the blood was demonstrated. Men like Gesner and Aldrovandus took up natural history studies where the Greeks left off. They found certain terms current—I am thinking especially of their practice in the insects—which they proceeded to apply in the sense of genera. They indicated but usually did not name the included species. In fact,

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the presence of species was felt in only the vaguest sort of fashion. John Ray, in the late seventeenth century, defined them with practically Linnaean rigor, but his *Historia Insectorum* (1710) showed him little more successful at their actual detection than his predecessors of a century before.

The species concept, then, represented the first great generalization of modern biology—biology at an eighteenth century level. It was a static preliminary generalization before evolutionary thought and the creation of the science of chemistry opened the way for biology's further development in the centuries that followed. "Static" and "eighteenth century" are fighting words in many vocabularies. Especially is this true in the case of biology, where evolutionism and the experimental method have resulted in such rich scientific harvests. But one is entitled to remember that these studies require the firm descriptive basis that it is the function of the species concept to give. And the fact that biologists perennially gather to discuss species is further evidence of the fundamental nature of the problem they present.

The human mind is fearfully and wonderfully formed. This is not strange if an attempt be made to ascertain its original function. For it does not appear that the mind is primarily an organ of reflection. Rather it arose in man when his every moment was one of action and peril. It flourished because it turned out that the mental way of meeting the exigencies of life was more efficient than the instinctive way. It is only in the late stages of its development that it becomes at times an organ of reflection. There was no leisure for primitive man to do much thinking. He had to generalize from his sense impressions in the shortest possible time an abstraction which he immediately proceeded to apply to the matter of meeting his biological requirements. The leap from the sense datum to the abstraction was of the briefest, and ill did it betide our cave ancestor if he pondered too long over the classification of the saber-tooth that was about to devour him.

The abstraction "fearful beast—run" was of the utmost urgency!

It is not surprising, then, that when man began to philosophize, he should have carried over this tendency to rapid abstraction. It was only gradually and at the expense of much labor that he learned the shortcomings of this instinctive method and the need for the slower, more painstaking and cautious analysis of his data. Nearly all thinkers have recognized the fact of induction; but for the early ones, even for Aristotle, it was a brief hurried affair for the establishment of generalizations, from which the procedure was deductive. Not that abstraction is to be deprecated. But let us not become lost in the maze of our abstractions and mistake it for our science.

I have told my students and some of my readers may have told theirs that individual animals and plants are brought together in logical union to form species, that these are similarly assembled to form genera, these to form families, and so on through the other categories of our classification till we get to the major inductions, the Plant and Animal Kingdoms. These lead to the final great induction, that of living matter itself. All very nice and proper, but so far beside the facts! The actual processes, both psychological and historical, are so utterly different. Only the very last step is actually an induction for most of us. That we struggle and toil over in our elementary biology classes, endeavoring to emerge with a unified concept of living things. All else is deduction and analysis. We arrive at the concept—animal, insect, bird—by a brief superficial induction, whereupon we proceed to divide and redivide, usually forgetting that it is only our concept we are analyzing.

One who will examine some of the works of Linnaeus and others of the early naturalists can see the species concept gradually developing in their hands. First there was a mere listing under a few generic heads. Then, as the material was more exhaustively studied, there came

an increase in both genera and species. This increase may well have alarmed its initiators, who saw slipping through their fingers the logical beauty of their initial system. But the day when such factors were paramount was past. Science had established itself firmly. The facts must be followed wherever they would lead.

With the increase in the number of species came a strain on the current method of designation, which consisted of the many-worded species formula. Then Linnaeus invented the species name, and modern species nomenclature was initiated. Like many great ideas, it was very simple after some one else had shown the way!

At first there were a few genera containing a few species. Both tended to be split up as the result of subsequent analysis. This is especially true of genera. Of course, *new* genera are frequently discovered, *i.e.*, genera based on species not previously included in previously described genera; but the vast proportion of our familiar genera have been split off from old ones. *New* species are more frequently discovered than new genera; but there, likewise, large numbers of species have come into being through a reanalysis of old specific concepts; and sometimes even the type series of an old species has been found to be composite.

The descriptive analysis of plants and animals is a complex affair requiring the application of many minds for its consummation. I have myself had the experience of giving long and careful study to a series of specimens that I suspected of being composite. I was led finally to the view that I had a single variable species; and then another author divided my "species" into four which I was at once able to recognize as indubitably valid!¹ Everything can not be discovered by one person in a single lifetime.

It is only in the mind of the relatively sophisticated taxonomist that taxonomy becomes a synthetic rather than an analytical process.

¹ Hatch, *Jour. N. Y. Ent. Soc.*, 41: 192-193, 1933; Fall, *l.c.*, 45: 335-340, 1937.

As a result of these more or less inevitable psychological tendencies, taxonomy was born with an overdose of abstraction. This was aided by the particular ideologies of some of the early taxonomists. Linnaeus,² for instance, explained that there were just as many species as were created in the beginning by the Creator. All that one had to do was to sally forth and discover the several types which were to-day just as the Deity had made them. Such teaching was extremely realistic in its logical implications, but Linnaeus was a good enough scientist and a poor enough logician so that the consequences were not pushed too far. The advance, however, of taxonomic analysis revealed the enormous practical difficulties standing in the way of the actual recognition of species. The result was that Darwin, in the second chapter of his "Origin of Species," was able to make a very effective, even though entirely formal, argument for evolution by exhibiting the contemporary disagreement among taxonomists as to what constituted a species and what a variety. Accordingly, Darwin reasoned, there was no difference, and, since the evolution of varieties from a common ancestor was admitted, it was necessary to grant the same of species.

With the advent of the evolutionary concept, it became necessary to give up the idea of the species as something ultimately real, related to other species, if at all, only in some logical transcendent fashion. In its stead was developed the familiar doctrine of the species as a stage in a continuously evolving evolutionary series. For the early Darwinians, in their heavy reliance on individual variation as the source of evolutionary change, the species must have become almost wraith-like in its consistency. With the subsequent discovery under experimental conditions that many species are relatively constant, some of the concept's previous substantiality returned; and it was seen that certain species, at any rate, are relatively stable and represent what is, at least, a plateau in the evolutionary process.

² "Philosophia Botanica," 1750, sec. 157.

On the practical side, however, the study of species remained in the post-Darwinian period much as it was before the introduction of evolution. The same temptations to over-abstraction exerted their influence and the same analytical processes were at work. The establishment of new species, genera and higher categories by the subdivision of old concepts rather than as the result of a new synthesis from the data themselves continued.

What, then, is the modern taxonomic concept of species?

Modern taxonomy has a dual aim: first, the description and classification of living things; second, their nomenclature. The one must not be confused with the other. Both are important; the two interact in a complex fashion; and with Linnaeus they may both have seemed to function as one. Then it was discovered that there was no self-evident natural system of classification. Subsequent study and other authors almost invariably introduce modifications in the system. Those who are familiar with the insects will recall that Fabricius, a student of Linnaeus, invented an entirely new set of ordinal names for insects because he had transferred the basis of their classification from wing structure to mouthparts. The tendency was, however, to conserve names, especially in the lower categories, and this was finally effected in the last century by the introduction of the type designation method. A genus consists of those species that are co-generic with the type species. A species consists of those specimens that are conspecific with the type specimen.

Moreover, as the result of such a procedure, the status of the definition has declined. Most of us have continued to attempt the definition of our categories. But for many years previous to 1931 it was possible under the zoological code to establish a new genus simply by the citation of a type species. This has now been corrected; but the validity of a generic or a specific name is almost literally completely independent of the definition. This has become almost a pure embellishment—a nice embellishment if we

happen to strike on the right characters, *i.e.*, characters agreed to by others—but utterly without importance if our successors happen upon what they believe to be a better definition. The result is that almost any combination of words will serve to establish a specific or a generic name.

The logical implications of such a procedure are nominalistic in the extreme. The taxonomist announces that there are no categories except those aggregates of the lesser categories brought together by him as a result of comparison with a type. It is a nominalism, however, which results from a procedure forced on the taxonomist as a result of his endeavor to stabilize his nomenclature. I am not, at this time, discussing nomenclatorial stability but rather the species concept that our nomenclature endeavors to express. Our nomenclatorial procedure represents, however, a healthy reaction to the over-abstraction of a previous period. And the extreme nominalism of our practice suggests that our theory may be similarly characterized. This is the question I would now consider.

With the advent of Darwinism, the old Linnaean realism is definitely *passé*. The species along with the other categories of our classification has been brought to earth from the transcendent realm of a Linnaeus or an Agassiz. The logic of their definition is not a transcendent one—that was just an error of misplaced abstraction. It is, rather, strictly imminent in the minds of the individual taxonomists. I am prepared to accept at least tentatively the extreme nominalism that our nomenclatorial procedure has indicated.

A further powerful nominalistic influence is represented by the absence of any general agreement among taxonomists as to the details of their classifications. In fact so inevitable does such disagreement seem that I venture to the generalization that, when two systems of classification are in agreement, it is *prima facie* evidence that one of the systems does not represent an original

study but is an uncritical compilation from the former. In connection with my teaching and my research I have made a study of categories at every level of our classification from kingdoms and phyla at the top to genera, species and varieties at the bottom. The structural features of the individual plants and animals are objective, and certain broad features of our classification are passed on from author to author. But, as to what the limits of the several categories are, as to just how much of a particular branch of the evolutionary tree is to be a phylum, a class, an order, a family, a genus, or a species, I find no fixed objective criteria whatsoever. These depend on the opinion, almost the whimsy, of the individual taxonomist, a fact that should be kept in mind when we are considering diverse classificatory systems. And I find rather cogent the suggestion made some years ago by J. C. Needham³ that the number of our categories above the species should be determined by psychological factors. How many units in our classification is it desirable to recognize? Let us recognize that many and make our divisions accordingly. Along the same line was the observation of the late J. M. Aldrich⁴ that when we increase the number of our genera we do not magnify the importance of the several included species, but merely debase the value of our generic units. And every one knows the futility of depreciating the currency!

A species is, primarily, composed of those specimens which, upon examination, the taxonomist believes to be conspecific. The crux of the whole situation lies right there. If you could pass on to me or I could pass on to you the criteria that we employ at this stage of our study in such a way that I would always agree with you on your species and you would always agree with me on mine—that would be a taxonomists' Utopia indeed! But this seems almost impossible of accomplishment.

A species is a series of individuals more closely resem-

³ *Science*, 71: 26-28, 1930.

⁴ *Science*, 65: 381-385, 1927.

bling each other than the individuals of any other species. That is a stock definition. The proviso is usually made that such variation as is involved shall be "continuous," whereupon the question becomes one of how great the breaks in the series can be and the variation still be so regarded. Again the matter is thrown back upon judgment.

One of America's ablest coleopterists, Henry C. Fall, died in 1939. During the past forty years he has described over fourteen hundred species of our Coleoptera, and he is given the high praise by his biographer⁵ of practically never having created a synonym. Which is to say that Dr. Fall's judgment was so developed that he instinctively cut through the maze of individual variation to the species itself, or rather to what his contemporaries are usually equally willing so to regard. He was, perhaps, in a position similar to that of the successful magazine editor who does no more than read a story and like it to know that a million readers will follow him in approval.

In contrast there is the instance of Colonel Thomas L. Casey,⁶ who in the forty years previous to 1924 described several thousand species of North American beetles. On every hand Colonel Casey's species have been criticized and queried, and large numbers of them have been put down as individual variants.

The matter is not, however, entirely so simple as might appear. Fall explains in at least one place⁷ that, in monographing the group, he did not attempt to place every specimen. A certain number of uniques would be left over which he could not locate with certainty in any of his described species, but which he did not feel warranted in recognizing as the types of additional species. It was, apparently, the study and description of this sort of material by Casey and his consequent establishment of large numbers of species on the basis of a scanty number of

⁵ Sherman, *Jour. N. Y. Ent. Soc.*, 48: 34, 1940.

⁶ On Casey see Hatch, *Ent. News*, 37: 175-179, 198-202, 1926.

⁷ P. 292 of his monograph on *Pachybrachys*, *Trans. Amer. Ent. Soc.*, 41: 291-486, 1915.

feebly differentiated specimens that led to some of the differences in the work of these two naturalists. Casey described numbers of tentative species. Some of the older entomologists are somewhat facetiously accused of tossing the occasional troublesome specimen out the window or grinding it on the floor under foot. There is no evidence that even the most conservative of contemporary naturalists do that. They have learned to treasure their exceptions as the key to future progress. But Dr. Fall's failure to publish some of this material resulted in much the same thing. While it enhanced the logical clarity of his dichotomies and probably made his work more acceptable and usable to his contemporaries, it accomplished this only at the price of the suppression of a part of the data. This does not, of course, exhaust the differences between the two types of work. Casey's concept of a species was an undeniably narrow one.

Before coming to objections that may be raised to a nominalistic interpretation of species, I should like to point out certain advantages that may accrue to such a position.

First, it keeps the mind centered on the individual data themselves, true to the spirit of modern science. It is thus operationalistic in its import, teaching one to confine his attention and efforts to things he can handle rather than to be chasing off after will-o'-the-wisps.

Second, it recognizes the categories as simply generalizations in the minds of the individual taxonomists. Disagreements, then, in classification are disagreements in opinion, and concerning disagreements in opinion, *de gustibus non est disputandum*—one must not argue concerning tastes. Not that opinion is unimportant. Man's whole weal or woe is tied up ultimately with opinion. Opinion can and must be discussed. Its factual basis must be examined and reexamined. But let it be remembered that it is opinion and that in science even more than in politics the mutual toleration of the other fellow's opinion is basic.

Now it may be seen whether there is not some way out of the extreme nominalistic impasse to which we have come. Some of the limitations of the analysis may already have been noted.

A species is a series of individuals. . . . Our species are mostly founded on dead preserved specimens. It is not, accordingly, inappropriate to remind ourselves that the "individuals" on which one establishes his species must be living organisms functioning and reproducing in an actual environment. Dead specimens are significant only as they represent such living organisms, and any induction based on such specimens is at least once removed from the living organisms themselves. I still remember the expression of dismay with which one of my students once countered that, if such were the case, I didn't have a single species in all the many boxes of my beetle collection!

One approaches the *sanctum sanctorum* of the living organism itself. I sometimes wonder if there is any entrance way at all to that mystery. The taxonomist defines to the minutest feather or seta. The ecologist traces the intricacies of the environment. The physiologist distinguishes compound after compound in every bodily function. The embryologist works out the stages in the development and the phylogenist those in the evolution. Yet, when all are through, the organism itself still eludes us. Aristotle called it an *entelechy*, an inner end, which we may define in terms of growth and reproduction: an organism is a system existing for its own increase and perpetuation. But I wonder whether the problem itself is not an improper one, one that in Kantian terminology transcends those limits of our reason that are imposed by our logical and psychological natures.

If such are the difficulties in connection with seeking the nature of a single living organism, what of those surrounding a group of such organisms like a species? One may suggest that the species is primarily the corollary of the attempt of the individual living organism, acting in

geological time, to extend itself to all possible habitats. It is, apparently, a by-product of the evolutionary process, an accidental concomitant of the circumstance that, as the living organism extends itself in time and space, the chain of its continuity with its predecessors becomes broken here and there. Species are the result. Again nominalism prevails. The initial, the sole mystery is the living organism. The species is the chance result of the individual's efforts to extend itself—just as I have been insisting from the beginning, an aggregate of individuals. But there is little original in such a view. Darwin had the essence of it seventy years ago.

At the basis of the present recognition of species is a comparison between specimens. Whether or not two specimens represent two species or one is ultimately a function of the judgment of the observer. May there not be some way to bypass the subjective element in this process?

One thinks at once of various physiological tests as the precipitin test for comparing body serums, of the statistical examination of data from series of specimens, or of supplemental data from a study of genitalia, of habits, or of ecological relationships. While it is true that a species is more validly established as more different things about it are observed, none of the methods mentioned escapes the fundamental limitation of the observational method, namely, the subjective comparison of phenomena.

The fertility-sterility test has frequently appealed to me as presenting an objective method of demonstrating species validity, a sort of experimental taxonomy. The basic assumption would be that two stocks are not conspecific if they are unable to hybridize or if they produce hybrids that are themselves sterile. Thus the horse and the ass are distinct species since the mule and the hinny are nearly always infertile. On the other hand, certain taxonomists, especially in ichthyology,⁸ recognize as distinct species certain morphologically differentiated stocks

⁸ Cf. Hubbs, *Aquatic Life*, 5: 101-103, 1920.

that usually do not in a state of nature interbreed, although capable of doing so.

On the whole, capacity to interbreed with fertile offspring must be regarded as very significant evidence in any consideration of the degree of consanguinity of closely similar stocks. Whenever such a test is applied, its verdict is conclusive, as long as one is reasonably sure that the specimens he is uniting or separating belong to the same stocks with which he originally experimented. One can never really escape from some reliance on direct observation!

It is because the possibility exists of such an objective test of species that one can look upon the species category as somewhat different from the categories above or below it in the scale. The other categories are dependent for their recognition upon direct subjective observation alone. Most species rest on this same basis—this is why I insist that the species problem is essentially the same as that involved in the other categories. But occasionally this other more direct test is available. And I look for an extensive future development of this experimental taxonomy.

Practically, however, we are limited by our resources of men and time and by our imperfect knowledge. This last keeps us from being able to maintain many animals under experimental conditions for the requisite series of generations. Think of the problems involved, for instance, in the experimental breeding of whales! The result is, at present, that we are unable to apply the fertility-sterility test to more than a few forms. As to the rest we must rely on direct observation. For species must be recognized and defined here and now, not next year or next decade!

Let us look at the matter in another way. I discover a new species. One, two, three, five specimens on the cork in front of me are the only examples known. Is the species those very examples? Or is it the description of those specimens that I publish? Or is it the more ade-

quate description of those and sufficiently similar specimens that one of my successors may some day publish when most of the species of that particular genus are known and when the description can be supplemented with detailed studies on physiology, genetics, ecology, etc.? Or are we on the wrong track altogether and is the species none of these things, but the sum total of all the sufficiently similar individuals of this type that are living, that have lived, or that will live, irrespective of any one's description?

The first of the questions can be disposed of without too much difficulty. Only the most naïve of taxonomists would insist in the face of even the briefest inquiry that the species is identical with the examples. I have, however, seen it asserted in print⁹ that certain authors had such and such species in their collections. This is a mere elliptical manner of speaking that does not bear analysis.

The last of the questions, to the effect that a species is the sum total of all similar individuals, can be thrown out on the grounds that it so completely transcends all possible human experience as to place the species beyond the bounds of human knowledge. Science must not set up for itself impossible tasks.

This leaves us with the two median questions: Is the species my description or is it the best possible description that human ingenuity can devise? Here again the second alternative involves a definition that, while it does not transcend all human experience, transcends present experience, and makes itself almost as objectionable as the fourth possibility that transcends all experience.

The species, then, is one thing and one thing only, namely, the concept that the taxonomist develops on the basis of his data, but with the important qualification that it is subject to modification as more data accumulate or as those data that we do have are better understood. In certain cases it will be revealed that a given species can

⁹ Fall, *Trans. Amer. Ent. Soc.*, 27: 300, 1901; "A Review of the North American Species of *Agabus*," p. 3, 1922.

not be maintained. Since we can never be positive that any one species under consideration will not someday be shown to be invalid, we can never possess absolute certainty about the validity of any given species. However, we do possess probability, and the more frequently a given species has been recognized the more likely is it to be valid.¹⁰

I hope that you are beginning to see something of the protean nature of the species as I feel that modern taxonomy conceives it. For we are too apt to assume that all species, like all men, are created equal! It is a fallacy that is likely to be committed from the circumstance that our specific names are nomenclatorially equal and from the superficial equality that our species are likely to assume as one arranges examples in his collection or as one orders his descriptions and diagnoses in a printed catalogue. It will be profitable then to pass in review some of the multifarious but legitimate meanings applying to the species concept.

(1) There is, first of all, the concept as it attaches to man. In fact the human race is the unique example of a species of this sort. We ourselves, being humans, know the human species both from without and from within. In fact, modern philosophy concludes that all our knowledge, all our learning, is just man's reaction to his world. On the purely biological side, even, our knowledge of *Homo sapiens* is extraordinarily complete. Of all the branches of descriptive biology, that of gross human anatomy comes nearest to being an exact science. And in embryology, physiology, pathology, and psychology our knowledge is far advanced. We know an enormous amount about the subspecies and races of man, something of his evolution, and considerable about his heredity. We have, then, in man the species concerning which our knowledge is most adequate.

(2) Next there is a group of species concerning which

¹⁰ I refer here to the biological validity of a given specific concept and not to the nomenclatorial validity of any single name.

we know a great deal. Our knowledge is far less complete than in the case of *Homo sapiens*, but it is still very extensive. I refer to species like the dog, the hog, domestic cattle, the domestic fowl, the honey bee, and, among plants, wheat, Indian corn, apple and many others. Under the influence of their contact with man, these species have broken up into many varieties. The fact that the professional taxonomist, at least in zoology, is somewhat uncertain as to just how to face these varieties must not obscure from us the circumstance that we are here in the presence of very well known specific types. If there is to be any uncertainty, it must be not in connection with these domestic forms but in connection with their wild relatives, concerning which, paradoxically, the taxonomists profess no doubt whatsoever!

(3) Continuing with the account of the different meanings of the species concept, we come next to a large group of well-known species. Less familiar than are man and the domestic animals, they are, however, abundantly known. The codling moth, the European corn-borer, the *Drosophila melanogaster* may be cited as examples—species which have been extensively studied in the living condition. Some of these are so important that thousands of dollars are spent every year in their study.

(4) Then there are the lesser known species—species about which something is known as living things, but which have never been studied in any very complete fashion. The lesser pests, species about which food plant or other ecological data are available, are included here.

(5) Next in descending order of adequacy are species that are well known to taxonomists but which have not been studied as living things. Such species are those that have been abundantly keyed and described by a succession of authors and are likely to be present in many different collections. Even the best-known fossil species do not rise above this level of our knowledge.

(6) Then there come those species that are adequately based, as on a sufficient series of specimens with a suffi-

ciently critical comparison with related species, but which have been studied by relatively few, perhaps by only one or two taxonomists, so that their formulation may still be unduly influenced by the limitations and idiosyncrasies of the personalities connected with them. A large percentage of our insect species, probably the great majority of those from the tropics, rise no higher than this level.

(7) After this are what should be regarded as tentative species. First are those having all the earmarks of validity, but founded on few specimens or even on a unique example. They are, on the face of the matter, adequately characterized. Especially where founded on a careful comparison with examples of related species and when accompanied by proper diagnostic keys to the related species, such species have a fairly satisfactory status.

(8) When, however, the species has been established by comparison with the published descriptions only of related species, without recourse to actual examples, the species attains a more tentative status. When published figures or photographs are available the difficulty is less, although nothing can really substitute for an actual specimen. When only a description is at hand, the difficulty of understanding it is frequently rather great. No description can really exhaust the specimens. While an accurate interpretation of printed descriptions is often made, often likewise the second author is likely to misinterpret or misunderstand the words of his predecessor, so that he comes to establish his species on the basis of supposed differences only that really do not exist. Such a procedure, with its attendant possibility for error, is likely with students who are working in more or less isolation from great collections. But so numerous have the described species of animals and plants become and so scattered the examples on which they are based that any worker anywhere is likely to find himself at one time or another forced to rely on descriptions. One can only use such judgment as one can and be ready to recognize one's errors as they appear.¹¹ On the other hand, one is en-

¹¹ I appear to have made some errors of this sort in my study of *Phaedon*

titled to remember that the species is essentially a concept and that, while in practice it can always be modified by reference to specimens, in theory the definition is intended to substitute for the specimens and bring out their peculiar characteristics, and until the definition has been modified one is entitled to accept it at its face value. A specific concept can be modified effectually by its redefinition under a new name even though that name is ultimately shown to be a synonym of the less adequately described species from which it is supposed to be distinct.

(9) Next there are species of a more tentative nature still, species that on the face of them are vaguely or inadequately defined. Many of the species described by Colonel Casey, who was mentioned above, are of this type, species among the beetles based on vague differences in general bodily shape or bodily proportions. Some of these may eventually be validated. Others, in the light of adequate series, will be shown to be individual variants.

(10) Then come species known from fragments. Students of the present-day flora and fauna have little to do with species of this sort, but they are inevitable and widespread in paleontology. Soft parts are always absent in fossils, but, obviously, where the neobiologist does not use them, the paleobiologist is at no disadvantage. Thus the fossil Foraminifera can be studied taxonomically with almost all the facility of living types, and the same can be said of many of the insect species represented by specimens imbedded in Baltic amber. In the Pelecypoda and Gastropoda, on the other hand, soft parts have been found to be basic for a proper understanding of recent species. The result is that the paleontologist would be at a disadvantage did not the very lavishness of his material compel the neobiologist to go to him as much as *vice versa*.

But it is when the paleontologist is working with a portion only of even the hard parts that the difficulties become especially acute. Odd plates, scales, teeth, bones,

(cf. Fall, *Pan-P. Ent.*, 5: 145-148, 1929) and in connection with some Helmidæ (cf. Hinton, *Ent. Mo. Mag.*, 75: 179-181, 1939).

wing-covers, always rise to plague the student of fossils.¹² Most of these, especially those from the more remote geological past, receive only a tentative placing; but frequently bolder assays are made. Errors as well as triumphs stand to the account of the paleontologist. If the fossil ape Henry Fairfield Osborn described from Colorado proved to be only the tooth of a pig,¹³ the Peking man, *Sinanthropus pekingensis*, was correctly diagnosed from an identical fragment.¹⁴

(11) Finally there are species that exist by circumstantial evidence alone. The track of a worm on a Cambrian sea-beach, the foot-print of a dinosaur from the Connecticut River valley, the tunnel of a beetle in a fossil log in Arizona—these are examples of species whose existence is attested to, but the details of whose structure remain obscure.

There have now been passed in review various meanings of the term species. It has been necessary to reject the more realistic interpretations on the ground that they transcend experience in an unwarranted fashion. There has been left a series of nominalistic meanings, ranging from very well-established species like man and the domestic animals, through the well-known species of the ordinary taxonomic study, down to those that are tentative only.

The next time the reader goes into the field or into his museum, the next time he takes up the study of a taxonomic treatise or is laboring on the preparation of a taxonomic work of his own, let him try as he proceeds to do a little philosophizing. First, let him remember that only the individual specimens have any reality. Secondly, let him not forget that he is doing the classifying—super-

¹² See Croneis, *Science*, 89: 314-315, 1939, for the proposal of a series of categories for use in classifying fossil remains whose true affinities are not ascertained.

¹³ Gregory, *Science*, 66: 579-581, 1927.

¹⁴ Described by Professor Davidson Black, of the Union Medical College in Peking: Keith, "New Discoveries Relating to the Antiquity of Man," p. 258, 1931.

imposing, as it were, logical forms of his own invention upon the heterogeneous material that he is studying. He has had predecessors, but let him not be dismayed if he does not agree with them or if his successors do not agree with him. Thirdly, let him remember not to be led astray by the nomenclatorial procedure that he as a law abiding taxonomist will find it expedient to use. Though equal in law, his species are far from equal in fact. What possible equality can there be between a species of continental distribution, on the one hand, and one confined to a single valley, an isolated mountain range, or a tiny island, on the other? Let him remember that many of his species will be tentative. He will be able, perhaps, to lay to rest some of the problematical forms of his predecessors, but he is likely to raise others with which to puzzle those that come after him. Let him remember, finally, that the main obligation of all science is to its data, and that a few data carefully marshalled are better than much questionable theory.

Accordingly, the species is no hard glistening tangible thing like the atom of classical physics. It is, rather, like the Schrödinger atom, a thing of mistiness and lack of definition. One can be fairly sure when one is getting pretty close to one, but never certain that one is actually there! Taxonomic relativity? Perhaps! But analogies must not be pushed too far.

A CONTRIBUTION TO THE THEORY OF EVOLUTION BY NATURAL SELECTION

JOSHUA L. BAILY, JR.

THE Darwinian conception of natural selection as the causative agent of organic evolution involves certain more or less reasonable postulates. The first of these is that all organisms tend to vary, that is, no two individuals are ever exactly alike. Secondly some of these variations are adaptive; they have survival value. And finally there is the Malthusian principle, that population pressure precipitates a struggle for existence in which the weaker individuals go to the wall. This is natural selection but it is not necessarily evolution. In order that evolution may occur two additional postulates must be stipulated. The first of these is that the favorable variations must be hereditary, for if they are not the individuals in each successive generation must begin just where their parents did, and there will not be any progress. Natural selection will not be effective. The other is that the environment itself must be in a state of flux. If the environment be rigidly static the effect of natural selection will be to check the course of evolution rather than to accelerate it, for the variations which will be selected for preservation will be those whose departure from the mode is least. But in a fluctuating environment the survival value of the mode may be subject to destruction; indeed if the environment be altered with sufficient rapidity the survival value of every variation may be destroyed, and the result will be not evolution but extinction. With a slowly changing environment, however, the organism may re-orientate itself about a new variation as a new mode.

It is greatly to Darwin's credit that he did not publish his theory until he had amassed a great quantity of corroborative evidence, but none of this evidence is really conclusive in so far that it does not furnish incontrovertible proof of the theory. Rather it is what a lawyer

would designate as presumptive evidence, because it merely creates a presumption in favor of the theory and puts the burden of proof on the critics. That Darwin himself appreciated this fact seems to be indicated by his having devoted two chapters of the "Origin" to meeting the objections which he anticipated would be advanced to disprove his theory. In these chapters he emphasizes the incomparable slowness of the process, which defies every ordinary technique of mensuration. To refer to a popular example, the giraffe did not acquire its long neck overnight. It needed several thousand generations, and although the final result is quite striking at no time have the differences between two successive generations or among the individuals of any single generation been other than exceedingly minute. Now it has been urged, and quite justifiably, I think, that minute differences of this order would not afford a foothold adequate for natural selection. If of two giraffes whose neck lengths differ by only a few millimeters that with the longer neck should survive, it seems hardly reasonable to suppose that this result could be attributed to any survival value of the greater neck length, although Darwin thought it might be. Rather, it seems to be not so much an illustration of the survival of the fittest as of what Dewar (1926) called "survival of the luckiest."

Among the followers of Darwin who accepted his theory but who nevertheless felt the force of this argument against it was Dr. Hermann C. Bumpus, director of the laboratory of the U. S. Fish Commission in the nineties. By a strange coincidence Bumpus had just given a lecture in which he expressed grave doubts as to the possibility of ever catching natural selection in the act, when, according to Vernon (1903), one of his assistants brought into his laboratory some material which seemed to supply a convincing demonstration of the operation of natural selection. This material was a series of English sparrows that had been disabled in a rainstorm. On these sparrows Bumpus made numerous biometrical measurements, such

as the lengths of the sternum, humerus, femur, etc., the breadth of the skull and the spread of the wings. After these measurements had been taken some of the sparrows had recovered sufficiently to fly away, while others succumbed. It was then observed that the sparrows which recovered were those which approximated most closely to the ideal form of sparrow hypothecated from the means of all the measurements. Conversely, those that died were the ones that departed most widely from the mean, regardless of whether the departure was positive or negative. It appeared that departure in either direction made for unfitness to survive.

When this conclusion was announced, it came in for a certain amount of adverse criticism. The critics argued that if a sparrow should have feathers of half the normal length, or of twice the normal length, its unfitness to survive would be obvious, but they felt that a departure of only a few millimeters would be too narrow a margin for natural selection to operate upon successfully. To meet such criticism, which has only a rational foundation, Bumpus could produce empirical evidence and ask what other interpretation could be put upon the figures.

A few years later Dr. W. F. R. Weldon, one of the editors of *Biometrika*, published some observations that seem to indicate a similar condition (Weldon, 1901-1902). Weldon's observations were made on shells of the land snail *Clausilia laminata*, of which he examined several hundred specimens. The outer lip of the aperture of this species, as in many other land snails, is sharp and thin during the adolescent period, but when full growth has been achieved the mantle edge continues to secrete calcareous material, so that the lip becomes thickened, reflexed, and denticulated. The form of the lip of a dead shell is therefore an approximate index of the biological age at which the snail died.

Weldon measured the peripheral radius of each shell and computed its coefficient of variability, both for the shells with thickened peristomes (which consequently

had lived a long time) and for those whose peristome was still sharp (indicating that the snail had died while young). The young snails were found to be significantly more variable than the adults, as if death were removing the more variable individuals before they could achieve full growth. Weldon's investigation seems more complete than that of Bumpus, inasmuch as the latter did not take into consideration the age of his sparrows. But Weldon's result may have another explanation—it may be that variability of the peripheral radius of *Clausilia laminata* decreases within the life span of the individual, just as Minot (1891), Shull (1905), and Pearl, Pepper, and Hagle (1907) had found to be the condition in the respective cases of the weight of guinea pigs, the shape of the leaves of *Sium cicutifolium* and the number of leaflets in successive whorls of *Ceratophyllum*. To test this possibility by eliminating any possible effect of natural selection, Weldon measured the peripheral radius of the shells with reflexed peristomes on their apical portions, which were formed when the snails were still quite young, and found the measurements so made not to differ significantly in variability from the homologous set of measurements made on those parts of the same shells that were formed at a later age. But both of these sets of measurements were found to be significantly less variable than that made on the shells of snails that died young, so that the conclusion that natural selection is effective in this case seems therefore inescapable.

But this conclusion, although based on empirical evidence like the earlier one of Bumpus, met with rational objections. Differences of the order of a few hundredths of a millimeter at most, it was argued, could hardly be considered adequate for natural selection to act upon, and to this criticism the same reply can be made as before by asking, Can the figures be interpreted in any other way?

The present writer believes that perhaps they can. The science of genetics, which was in its infancy when

Bumpus and Weldon were making their investigations, suggests another interpretation. The gene theory supplies a mechanism to account for the correlation of different characteristics. According to this theory a characteristic that has no survival value in itself may nevertheless reap the benefit of natural selection if it be correlated with another characteristic which is adaptive. Such characteristics are like the bills that get through Congress without any visible means of support. In such cases the sponsor of an unpopular bill merely attaches it as an amendment to another bill whose passage is assured, with which it rides through Congress unimpeded, like the wren in Grimm's fairy tale that concealed itself in the feathers of the eagle.

According to this view certain lengths of wing feather or of peripheral radius may be preserved, not because they have any survival value in themselves, but because they may be correlated with characteristics that do. The present writer feels that the failure of Bumpus and Weldon to detect any such characteristics with sufficiently wide variability was due to the use of unfavorable material. The sparrows in question were in a very abnormal condition—their physiological processes were suspended. The shells were dead and had no physiology.

Now the physiology and the morphology of an organism are as inseparable as corned beef and cabbage. Any picture of an organism that considers its morphology alone tells only half the story. In order to know an organism intimately both aspects must be taken into consideration.

The only investigation of variability in which both morphology and physiology have been stressed that the present writer feels competent to discuss is one of his own. The conclusions to which he was led at that time have been published elsewhere (Baily, 1939), and need not be recapitulated here. Since the appearance of that publication, however, many readers have offered comments suggesting that the possibilities of the investigation had not been exhausted in the published report, and the present

discussion is the outcome of a reexamination of the investigation in the light of those suggestions.

The investigation referred to involved the raising in the laboratory of a considerable number of pond snails of the species *Lymnaea columella*, each one in complete isolation from the day it was hatched. The parent stock was obtained from two ponds about 100 miles apart, one in Fairmount Park in Philadelphia, and the other near Pikesville, Maryland.

Every five days during the life of each snail the length of the aperture of the shell was measured, and the number of eggs laid by each snail during the five-day period was counted. The counting of these eggs was no mean task. The writer and his wife together counted over four hundred fifty thousand snail's eggs under the microscope.

Now the length of the aperture of the shell is a morphological feature, but the number of eggs laid in an interval of time is essentially physiological. In view of all the foregoing, therefore, the following questions naturally suggest themselves:

First, how does the physiology of *Lymnaea columella* as indicated by its fecundity compare in variability with its morphology as indicated by its aperture length?

Second, Can any survival value be ascribed to its physiological variation as represented by its fecundity?

Third, To what extent, if any, are the two variables correlated?

Fourth, Is the aperture length hereditary?

These four questions may now be considered separately.

1. It is clear that at any age there are at least two possible indices of fecundity. One of these is the total number of eggs laid up to that age, which number was called the established fecundity of that age in the investigation referred to. The other is the rate at which eggs are being laid—approximated by taking the eggs produced in the five-day interval since the preceding egg count was made. This latter index is in theory the derivative of the former.

Since either one of these indices may conceivably reveal

conditions that the other does not, it was felt advisable to compute the coefficient of variation at the end of each five-day interval for both the established fecundity and the fecundity rate.

These coefficients, together with those for the aperture length, are set out in Tables 1 and 2, for the Pikesville and Fairmount snails, respectively. Naturally no coefficients

TABLE 1
COEFFICIENTS OF VARIATION OF SNAILS FROM PIKESVILLE

Age	Number of snails	Coefficients of variation		
		Aperture length	Fecundity rate	Established fecundity
55	20	12.504 ± .108	192.56 ± .31	192.56 ± .31
60	20	13.097 ± .108	314.50 ± .49	170.12 ± .28
65	21	12.397 ± .106	227.81 ± .35	168.78 ± .27
70	21	12.391 ± .106	162.01 ± .26	146.53 ± .24
75	20	12.296 ± .109	151.69 ± .25	139.42 ± .24
80	21	12.073 ± .106	126.24 ± .21	126.05 ± .21
85	23	11.300 ± .101	140.88 ± .22	130.80 ± .21
90	26	10.426 ± .095	141.06 ± .21	129.81 ± .20
95	25	8.537 ± .096	135.82 ± .21	125.13 ± .19
100	26	8.014 ± .094	105.81 ± .17	114.13 ± .18
105	27	6.567 ± .092	83.82 ± .14	92.62 ± .15
110	28	6.005 ± .090	80.57 ± .14	93.12 ± .15
115	28	5.487 ± .090	71.84 ± .13	87.11 ± .14
120	27	5.507 ± .092	63.08 ± .13	82.02 ± .14
125	25	5.411 ± .096	57.33 ± .13	76.05 ± .12
130	23	5.380 ± .096	53.14 ± .12	70.84 ± .14
135	20	5.346 ± .107	48.53 ± .13	72.57 ± .15
140	18	5.531 ± .113	64.68 ± .15	81.58 ± .17
145	14	4.530 ± .113	39.14 ± .13	53.91 ± .14
150	14	4.597 ± .113	45.01 ± .13	62.20 ± .15
155	14	4.313 ± .113	53.98 ± .14	54.76 ± .14
160	14	4.149 ± .113	58.83 ± .15	48.50 ± .14
165	12	4.981 ± .138	57.92 ± .18	42.43 ± .16
170	11	4.805 ± .144	55.05 ± .18	35.43 ± .16
175	11	4.604 ± .144	56.28 ± .18	33.18 ± .16
180	10	3.758 ± .151	39.19 ± .17	28.23 ± .16
185	10	3.992 ± .151	38.08 ± .17	27.05 ± .16
190	11	3.890 ± .144	50.95 ± .18	25.90 ± .15

were computed for ages earlier than that of the first oviposition in each series, and none were computed for the later ages when there were less than ten snails surviving, for conclusions based on so few observations are not trustworthy.

Reference to these tables discloses that there is no substantial difference in either series between the two indices of fecundity as regards variability, but that both series are much less variable with respect to the aperture length. In the Fairmount snails the physiological variability is at every age over five times as great as the morphological

variability, while in the Pikesville snails it is over ten times as great. Natural selection therefore seems far more likely to eliminate the unfit individuals on a physiological rather than on a morphological basis.

2. In the investigation referred to (Baily, 1939) the following procedure was resorted to in order to test the survival value of fecundity. The established fecundity

TABLE 2
COEFFICIENTS OF VARIATION OF SNAILS FROM FAIRMOUNT PARK

Age	Number of snails	Coefficients of variation		
		Aperture length	Fecundity rate	Established fecundity
40	48	22.694 ± .072	685.56 ± .67	685.56 ± .67
45	49	21.292 ± .071	349.18 ± .34	371.53 ± .36
50	50	19.448 ± .070	204.07 ± .21	199.29 ± .20
55	50	15.441 ± .069	148.34 ± .16	142.56 ± .12
60	53	13.626 ± .067	92.94 ± .11	99.76 ± .11
65	53	12.487 ± .067	84.73 ± .10	84.99 ± .10
70	54	12.818 ± .066	76.88 ± .10	75.22 ± .09
75	53	11.020 ± .066	68.35 ± .09	71.64 ± .09
80	53	10.651 ± .066	67.24 ± .09	50.55 ± .08
85	53	10.043 ± .066	52.77 ± .08	60.54 ± .09
90	52	9.534 ± .067	60.55 ± .09	57.62 ± .09
95	49	9.106 ± .069	51.89 ± .08	53.62 ± .09
100	47	9.005 ± .070	48.50 ± .08	52.68 ± .09
105	46	9.573 ± .071	54.69 ± .09	46.08 ± .09
110	43	8.112 ± .073	56.32 ± .09	48.96 ± .09
115	41	7.536 ± .075	62.32 ± .10	45.95 ± .09
120	39	7.136 ± .077	58.98 ± .10	40.92 ± .09
125	35	6.484 ± .081	66.09 ± .11	37.32 ± .09
130	35	6.346 ± .081	57.47 ± .10	34.75 ± .09
135	29	6.056 ± .089	54.07 ± .11	34.35 ± .10
140	24	6.380 ± .094	63.87 ± .13	33.59 ± .10
145	21	6.549 ± .105	61.01 ± .14	29.64 ± .11
150	16	6.555 ± .120	76.28 ± .18	30.10 ± .13
155	12	4.674 ± .114	96.62 ± .19	29.20 ± .13

of each snail at death was compared with the mean established fecundity at the same age of the snails that survived that age. The difference between the two was then expressed as a proportion of the mean. The difference will be positive or negative according to whether the snail that dies is more or less fecund than those which survive.

If the differences are conspicuously inclined to be negative it may be safely assumed that the snails of low fecundity are being eliminated by death, but no such trend occurs. The index of selectivity of death is positive about as often as not, but not more so, and the two signs are scattered about irregularly at various ages. There is no evidence that any selection relative to fecundity is taking

place. At any age the super-fecund snails are just as likely, but not more so, to die as the sub-fecund snails.

But the fact that sub- and super-fecund snails tend to die at the same ages does not mean that they will contribute equally to the coming generation. The super-fecund snails will always produce a larger proportion *per capita* of the coming generation merely because they *are* more fecund, and the young snail will always have a better chance of having been "born" to a super- than to a sub-fecund parent. Therefore if the situation be looked at from the standpoint of the filial, instead of the parental generation, it will appear that fecundity *does* have survival value.

3. The coefficients of correlation between the indices of morphological and physiological variation were computed for the same ages as for those of variation, and set out in Tables 3 and 4. Reference to these tables shows that these coefficients are preponderantly positive.

TABLE 3
COEFFICIENTS OF CORRELATION OF SNAILS FROM PIKESVILLE

Age	Number of snails	Coefficients of correlation of aperture length with	
		Fecundity rate	Established fecundity
55	20	.42 ± .12	.42 ± .12
60	20	.26 ± .14	.47 ± .12
65	21	.36 ± .13	.49 ± .11
70	21	.54 ± .10	.67 ± .08
75	20	.59 ± .10	.62 ± .09
80	21	.68 ± .08	.69 ± .08
85	23	.66 ± .08	.68 ± .08
90	26	.60 ± .09	.60 ± .08
95	25	.57 ± .09	.55 ± .09
100	26	.57 ± .09	.50 ± .10
105	27	.41 ± .11	.45 ± .10
110	28	.51 ± .09	.32 ± .11
115	28	.33 ± .11	.20 ± .12
120	27	.36 ± .11	.22 ± .12
125	25	.11 ± .13	.11 ± .13
130	23	.03 ± .14	.06 ± .14
135	20	-.003 ± .151	-.03 ± .15
140	18	.22 ± .15	-.08 ± .16
145	14	.38 ± .15	.08 ± .18
150	14	.57 ± .12	.03 ± .18
155	14	.36 ± .16	-.09 ± .18
160	14	.64 ± .11	-.12 ± .18
165	12	.33 ± .17	-.08 ± .19
170	11	.51 ± .15	.07 ± .20
175	11	.63 ± .12	.09 ± .20
180	10	.10 ± .21	.71 ± .11
185	10	-.02 ± .21	.66 ± .12
190	11	.26 ± .19	.66 ± .11

Among the Pikesville snails there are only seven negative coefficients out of fifty-six, while of fifty coefficients in the Fairmount series none was negative. This proportion is too low to be considered fortuitous. Further it may be observed that all the negative coefficients have absolute values less than their own probable errors, while many of the positive coefficients exceed their probable errors by such large margins that they must be considered significant.

TABLE 4
COEFFICIENTS OF CORRELATION OF SNAILS FROM FAIRMOUNT PARK

Age	Number of snails	Coefficients of correlation of aperture length with	
		Fecundity rate	Established fecundity
40	48	.16 ± .09	.15 ± .09
45	49	.25 ± .09	.25 ± .09
50	50	.33 ± .09	.36 ± .08
55	50	.50 ± .07	.51 ± .07
60	53	.55 ± .06	.95 ± .01
65	53	.71 ± .05	.65 ± .05
70	54	.81 ± .03	.64 ± .05
75	53	.72 ± .04	.92 ± .01
80	53	.57 ± .06	.89 ± .02
85	53	.93 ± .01	.68 ± .05
90	52	.47 ± .07	.63 ± .06
95	49	.66 ± .05	.69 ± .05
100	47	.74 ± .05	.72 ± .05
105	46	.87 ± .02	.72 ± .05
110	43	.35 ± .06	.65 ± .10
115	41	.19 ± .10	.61 ± .07
120	39	.16 ± .11	.57 ± .07
125	35	.27 ± .11	.54 ± .08
130	35	.25 ± .11	.73 ± .05
135	29	.05 ± .12	.45 ± .10
140	24	.71 ± .07	.47 ± .11
145	21	.10 ± .15	.49 ± .11
150	16	.13 ± .17	.46 ± .13
155	12	.23 ± .18	.44 ± .16

At first sight this conclusion will appear inconsistent with that reached in the investigation hereinabove referred to (Baily, 1939), to which the present discussion bears a supplementary relation. In the earlier work it was concluded that no significant correlation could be detected between limiting shell size and total fecundity. It is difficult to see why this should have been the case if at all younger ages there is a real relationship between the two variables, and the apparent inconsistency must be accounted for before proceeding to the discussion of other matters.

Although in both investigations aperture length was correlated with fecundity, the two pairs of variables were not exactly parallel, since *total* fecundity and *limiting* shell size can not be evaluated in those snails that died before the symptoms of approaching senility developed. For this reason comparatively few snails were available for the earlier investigation of this relationship, and even though the coefficients of correlation based upon them might be comparable in magnitude to those in the present investigation their probable errors would be correspondingly so much higher that they could not be considered significant. Another disturbing factor is that symptoms of senility do not always appear at the same age. If the coefficients of a partial correlation in which the ages of the snails at death were held constant had been computed in the earlier investigation it is conceivable that they might have told a different story.

It must also be remembered that in a preliminary investigation based on a single clutch of eggs (Baily, 1931), the possibility of correlation between limiting shell size and fecundity was indicated. The writer hopes to consider this matter further at another time.

4. Our knowledge of heredity in pond snails is practically non-existent. Outside of some inconclusive references to this subject by Crabb (1927) and the Winsors (1935) the writer has been unable to find any mention of the subject in scientific literature except by Colton and Pennypacker (1934). These authors report that in a strain of *Lymnaea columella* that had been kept going for twenty years in their laboratory during which time nearly one hundred generations were produced, there was observed a slight but distinct tendency toward evolutionary modification of shell shape. Since Colton's index of shell shape involved the length of the aperture it is difficult to see how such change in shape could have occurred unless aperture length itself was hereditary. Yet Colton himself informs the writer that *Lymnaea* has undergone practically no evolution since the Cretaceous.

This lack of direct evidence is the weakest link in the hypothesis that natural selection is chiefly physiological. What has been shown is that this snail is in some respects more variable physiologically than morphologically, that some of its physiological variations have survival value, and that its morphological and physiological variations are probably correlated. That snails with longer apertures contribute a greater proportion of individuals to the filial generation than they themselves constituted in the parental generation seems established beyond any possibility of reasonable doubt, but we do not know that the snails are undergoing evolution in the direction of increased aperture length because we do not know that this trait is hereditary. About all we can say is the stage is set for this kind of evolution.

Yet it is not unreasonable to suppose that natural selection acts in just this way. It is difficult to imagine a structural modification that does not affect some physiological activity. The giraffe's long neck enables it to reach the higher branches of trees and the lower levels of water holes. A giraffe with an abnormally short neck would be morphologically unfit, but the unfitness would operate by impeding the physiological process of alimentation.

Many text-books of paleontology refer to the disappearance of the nautiloid cephalopods at the end of the Carboniferous as a great mystery. Here was perhaps the most highly specialized form of animal life yet evolved dominating the sea. Yet with the exception of a few species living in the South Seas to-day nearly all of them became extinct at about the same time (Zittel, 1927). If this came about as the result of the sudden introduction of a new factor into the environment how did the recent species of *Nautilus* escape a similar destruction? There is no conspicuous morphological difference between the recent and most of the extinct forms.

But on the supposition that their elimination may have been the result of physiological unfitness, the mystery of their disappearance ceases to be surprising, though it is

not dispelled. We know nothing about the physiology of the palaeozoic nautiloids, and as long as conditions are unknown contingent results should not astonish us. Later in the Cretaceous a somewhat similar occurrence took place. In this period the world of life was dominated by the reptiles of which eleven different orders are recognized. Then suddenly seven of these were extinguished without progeny. The commonly accepted explanation is that they were crowded out by the rising generation of mammals. But even if this be a correct statement it can hardly be considered an adequate explanation. How could a generalized form, such as the primitive mammals were, descended from the most primitive reptiles, compete successfully for survival with the most highly specialized members of that class, who seem to have achieved practically perfect adaptation to their environment?

Not until the physiology of recent reptiles is considered is it possible to account for the fate of their Mesozoic relatives. The reptiles are poikilothermal; on the approach of cold weather they assume a state of torpor in which they are easy prey for their enemies. Also most reptiles do not guard their eggs; many indeed do not even see them, but abandon them to nature so that they are likely to fall victim to marauders.

One would think that the California condor, with perhaps the most acute vision yet evolved in the animal kingdom, practically unlimited capacity for sustained flight (one authority believes it can remain in the air for several days, Hess, 1930), and great muscular strength of mandible and talon would represent the acme of adaptation to its environment. Instead the condor is rapidly traversing the path over which the nautiloids and the dinosaurs have already vanished, and to-day there are probably not as many as twenty-five pairs of condors living in the wild state. The reason is that the condor is a physiological misfit. It is too particular about its food. Although exclusively carnivorous it does not kill its prey as the hawks and owls do, nor does it eat meat in a desic-

cated condition like the turkey vulture. It demands freshly killed meat (Taylor, 1859a; James, 1906).

Also the condor does not breed in successive seasons, and when it does but a single egg is produced (Taylor, 1859). The period of incubation is not known with any degree of exactitude, but J. R. Pemberton informs me that from his own observations it appears to exceed six weeks, and that the young bird remains in the nest until it is at least six months old. He also believes that the adolescent period is three years, and that during its adolescence the chick is dependent upon the care of the parent birds, so that the latter are unable to breed again until the young bird is sexually mature. This is not known with certainty, but it seems to be confirmed by circumstantial evidence. Note how much better qualified physiologically for survival is the quail, which Clinton G. Abbott tells me lays anywhere from six to twenty eggs in a clutch, whose period of incubation is only three weeks, and whose young leave the nest almost immediately on hatching and require but a single season to achieve sexual maturity.

And while thinking of quail, consider the difference between those of the two continental coastal plains. A westerner beholding for the first time an eastern quail would recognize it at once by its morphological resemblance to its western relative. But if before seeing it he should hear it sing this physiological manifestation would hardly suffice to demonstrate to him its close relationship to the bird with which he was acquainted. The same thing is true of the meadowlark. Similarly, any observer other than an experienced ornithologist might have difficulty in distinguishing by sight between a crow and a raven, or between a night hawk and a whip-poor-will, but any doubt as to the identification of these birds would be dispelled at once by their voices.

The morphological traits that enable the desert sidewinder to be distinguished from other rattlesnakes are fairly conspicuous, but they are not nearly so obvious as the peculiar method of locomotion which is a physiolog-

ical trait. Another instance from herpetology is the speckled rattlesnake *Crotalus mitchellii* s. s. and *Crotalus mitchellii pyrrhus*. Although originally described as separate species these have long been considered identical until Klauber (1936) showed that they were distinguishable, but only subspecifically, on morphological grounds. But there seems to be a great difference in the toxicity of the venoms, which is distinctly a physiological trait. *C. mitchellii* s. s. has an MLD of 0.04 as against 0.50 for *C. m. pyrrhus*. (The MLD, according to Klauber, *loc. cit.*, is the fatal dose for a pigeon of 350 g. weight.) It is not clear whether this great difference is due to difference in chemical composition or to a different degree of dilution.

For another instance of venom differentiation I am indebted to Dr. Emmitt R. Dunn, who tells me that *Bothrops nasuta* in Costa Rica may develop either one or two types of venom, one like that of the same species found elsewhere, and one like that *B. ophryomegas*. Dr. Dunn has not published this item, but he has kindly allowed me to make use of it.

The well-known case of the fruit-fly *Drosophila pseudoobscura* is similar. Two geographic races of this species are recognized, whose only morphological difference is the size and shape of the *y* chromosome (Lancefield, 1929), but which differ in the duration of the developmental stages and rate of oviposition (Shapiro, 1932) and their physiological reactions (Dobzhansky, 1935).

Semeniuk (1940) has reported his own observation of at least two physiological races of *Ustilago hordei* which differ only in host specificity. But he also states that eight different physiological races of this parasite have been recognized by other authorities.

Robson (1928) and Robson and Richards (1940) record a great multiplicity of physiological races whose discrimination on morphological grounds alone is attended with great difficulty or may even be impossible. Their examples are drawn not only from the metazoa, but from

the protozoa, the fungi, and the bacteria as well, and the references are amply documented.

The human species supplies several examples of physiological variation unaccompanied by any easily observable corresponding morphological modification. One of the most interesting of these comes from the field of mental medicine. Overholser (1939) reports that three of the most common mental disorders, dementia praecox, paranoia and manic depression, can not with any certainty be attributed to any defect in the brain or nervous system. It is difficult to believe that no such defect exists, but the fact remains that if it does it has not yet been positively identified.

Dr. William E. Ritter has called the writer's attention to the fact that there is no structural difference between the hands of those Indians who make baskets and of those who make pottery. For that matter, every pueblo in New Mexico is characterized by its own peculiar type of pottery, which might well be considered as so many different instances of physiological differentiation. And there is also probably no infallible criterion by which the hands of a violinist may be distinguished in advance from those of a pianist.

The story of how a large number of human beings were eliminated as unfit by a physiological defect entirely dissociated with any morphological modification is related in the following words of the Old Testament:

Then Jephthah mustered all the men of Gilead, and fought Ephraim; the men of Gilead routed Ephraim, and Gilead seized the fords of the Jordan to check Ephraim; whenever a fugitive from Ephraim said "Let me cross," the men of Gilead would ask him, "Are you an Ephraimite?" If he said "No," they said to him "Then say 'Shibboleth'"; if he said "Sibboleth," if he could not pronounce the word correctly, they seized him and slew him at the fords of Jordan. So perished forty-two thousand men of Ephraim. (Moffatt, 1922.)

From these miscellaneous instances it appears that in many organisms physiological variation is more pronounced than morphological variation. And even in those cases where considerable morphological variation

occurs the elimination of unfit individuals by the action of natural selection may prove in the final analysis to be physiological. Instances of correlation between physiological and morphological variation are naturally more difficult to come by. For this reason the writer desires to solicit the cooperation of any investigator who may read these lines. He would be most grateful to receive any bibliographic reference to the variation, the survival value, or the correlation with morphological features of any physiological trait of any organism. He believes that the great contribution of the future to the theory of evolution by natural selection will come from the field of experimental physiology.

For assistance in the preparation of this article grateful acknowledgment is due to Dr. Francis B. Sumner, Dr. Leonhard Stejneger, Dr. Henry S. Pratt, Mr. J. R. Pemberton, Mr. Laurence M. Klauber, Mr. Phil Townsend Hanna, Dr. Denis L. Fox, Dr. Emmitt R. Dunn, Dr. Raymond L. Ditmars, Dr. Charles M. Bogert, Mrs. Ruth Ingersoll Baily and Mr. Clinton G. Abbott.

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REGIONAL DIFFERENTIATION IN PLANT SPECIES¹

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GENERAL RELATIONS BETWEEN PLANT AND CLIMATE

MANY species complexes of plants have an extremely wide vertical or horizontal distribution. Such complexes show a remarkable diversity of form and reactions that must be understood before a proper classification can be presented, and, more important, before the organization of the living world can be fully interpreted. Examples of such complexes are *Potentilla glandulosa*, *Achillea millefolium* and *Artemisia vulgaris*, all of which cover a large part of California from near sea level to around 11,000 feet altitude, and in addition have representatives circling the Northern Hemisphere.

The climates in which their California members live range from warm temperate to arctic-alpine. The weather graphs in Fig. 1 describe the climatic differences in such a transect across central California. The lowermost graph describes the climate in the mild, warm temperate, coastal region, where freezing temperatures occur only during a very limited period and continuous growth is possible for many herbaceous species. The center graph gives similar information for a locality midway up the western slope of the Sierra Nevada, at 4,600 feet altitude, where winters are cold enough to force most plants into dormancy for five or six months of the year. The uppermost graph presents data from a station near the crest of the Sierra Nevada at 9,600 feet altitude, and although it does not represent the extreme conditions found among the peaks, it does give an idea of the climate in the high mountains.

Plants of the same or closely related species from cli-

¹ Read at the Seattle symposium by Dr. Keck.

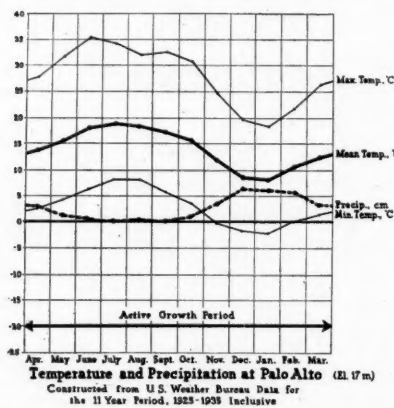
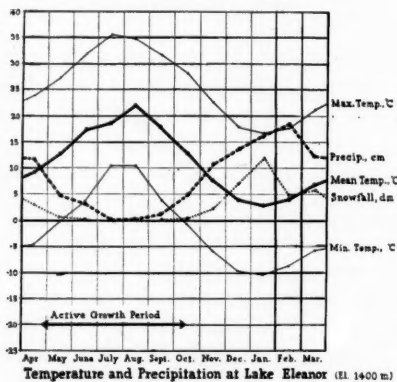
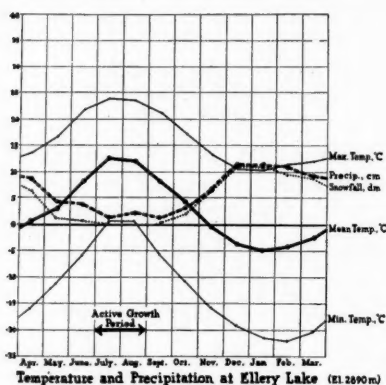


FIG. 1. Weather data from three stations on a transect across central California.

mates so unlike as the California coast and the high Sierra Nevada are very different in appearance and reactions. The alpine generally differ from their lowland relatives in size and other morphological characters, and also in their rate of growth, earliness, frost-resistance and other ways physiological. Series of intermediate forms connect the extremes.

Many questions arise concerning the nature of climatic forms: Are they due to the direct impact of the environment, and hence to be regarded as modifications, or are they hereditary in nature? Is it possible to change lowland forms into alpine by transferring them to the alpine environment as Bonnier (1895, 1920) reported, or do lowland and alpine forms remain distinct when grown side by side in a uniform environment as Kerner (1891) and Turesson (1925) found? If the differences are hereditary, what is their nature? Are they purely morphological, or are physiological characters also involved? If so, is each climatic belt populated with a race especially fitted to survive there? Finally, cytologists and geneticists raise other questions concerning possible chromosomal differences in such forms, the possibility of free exchange of genes in offspring of crossings between plants native to contrasting environments and the vigor of any such offspring.

In order to clarify such questions as these, the Carnegie Institution of Washington undertook an investigation in which experiment stations were established in three very unlike climates in central California. The principal station is located on the San Francisco peninsula, near sea level, at Stanford University. The second is at Mather, near the western boundary of Yosemite National Park, at 4,600 feet elevation, and the third is situated near Timberline just east of the crest of the Sierra Nevada, at 10,000 feet elevation, in Mono County. The contrast between the climates at the three stations is striking, as shown by the weather graphs of Fig. 1, which were constructed from U. S. Weather Bureau data obtained near

the three experiment stations. At Stanford, the growth period for plants is ordinarily continuous the year around; at Mather, it is approximately six months long; while at Timberline, it is shortened to approximately three months. At the alpine station snows usually persist in the gardens until the first of July, and there are but three to six weeks of relatively frost-free weather.

Into the gardens of these three stations representatives of many climatic races from the Pacific Coast region were brought for an analysis of their reactions. Species from a wide range of plant families were used. Perennials only were employed, for this made it possible to propagate them asexually and grow parts of one individual simultaneously at the three climatically very unlike stations. This permitted a two-way comparison. Genetic variation was eliminated by comparing divisions of one individual grown in three contrasting environments, so the differences observed were due to environmental modification alone. On the other hand, by bringing races of the same or related species from contrasting environments into a uniform garden at one station, gross environmental differences were eliminated, and the hereditary differences between them could be compared. Systematic records in the form of yearly herbarium specimens, measurements and notes made it possible to study the plants in detail through a number of consecutive years. An analysis of these experiments, which were inaugurated by the late Dr. H. M. Hall, has recently appeared (Clausen, Keck and Hiesey, 1940).

From these experiments it is clear that the variations which one observes in wild plants are of two sorts: those due to hereditary differences and those due to environmental modifications. Both contribute to the complex differences observed, not only in comparisons between climatic or geographic races, but also between competing individuals of the same population.

Each species of wide distribution consists of an assemblage of biotypes and races, some local, others of higher

order and regional. Species are usually broken up into intermittent populations because of environmental conditions. Each population consists of minor local variants or biotypes, but its members as a whole share characteristic morphological traits that frequently serve to distinguish this population from others of the same species. The frequent development of the local population into a recognizable morphological-geographical unit is probably the result of partial geographic isolation alone. The local differentiation appears to be of no major importance for survival in a given habitat, for individuals from different populations in one climatic belt follow the same general pattern of reactions and survival when transplanted to the different climates of the transplant stations. However, plants from the same population have been found to show slight individual differences in their reactions to these contrasting environments.

A very different situation is uncovered when representatives of races native to climatically different belts are analyzed by the transplant method. Such races do not react alike at the transplant stations. They differ much in their periods of activity, time of flowering and capacity to survive at the stations. These reactions are correlated with the environment in which they are native, and plants of different families but from the same general climatic belt show basically similar reactions.

By classifying the plants as to their reactions in the different climatic gardens, it is possible to recognize several major or regional climatic races that recur with frequency in various genera and families. These correspond roughly to the major life zones, which are, of course, a biotic expression of climatic differences. It takes about five to seven major climatic races of a species to occupy the entire climatically diverse region across central California.

Like the life zones, regional climatic races replace one another in the territory occupied by the species. They are most homogeneous toward the center of their distribution, but frequently intergrade through hybridization

where they meet or even overlap. Sometimes observed differences in reaction between races can be correlated with morphological differences, thus providing markers for delimiting the climatic races quickly in herbaria after such a correlation has been established by experiment.

POTENTILLA GLANDULOSA

An example of a species differentiated into climatic races is shown in Figs. 2 and 3. This is *Potentilla glandu-*

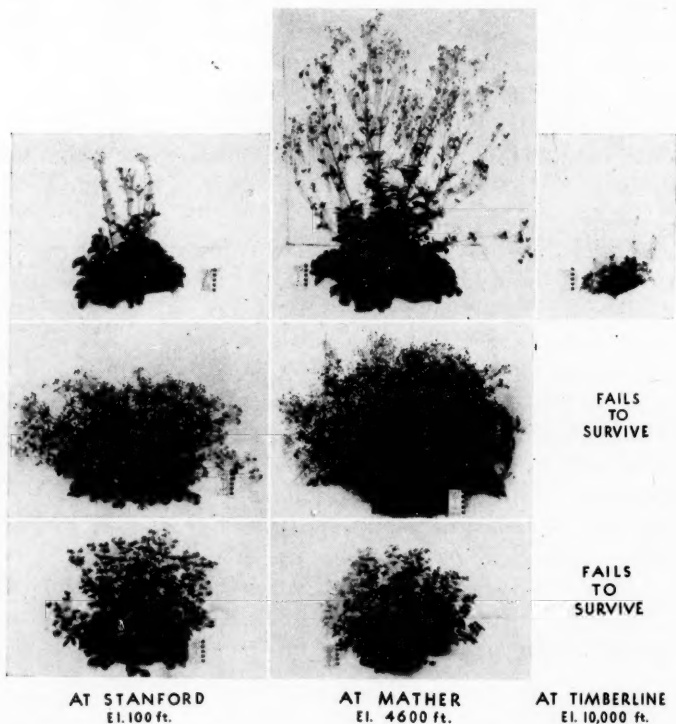


FIG. 2. Clones of three climatic races of *Potentilla glandulosa*. Lower row: plant of the Coast Range race, ssp. *typica*, from 600 ft. altitude; center row: the Sierran foothill race, ssp. *reflexa*, from 2,500 ft.; upper row: the mid-Sierran meadow race, ssp. *Hanseni*, from 4,600 ft. Horizontal rows show modifications of one individual at three transplant stations. Vertical rows show differences between races at any one station.

losa Lindl., of the rose family, whose California representatives are distributed from near the seacoast to about 11,000 feet elevation in the Sierra Nevada. The horizontal rows in the two figures represent divisions (clone-members) of individuals transplanted to the three stations. The differences seen between members of one clone are modifications imposed by the contrasting environments. The five individuals in the two figures were native at different elevations, as follows.

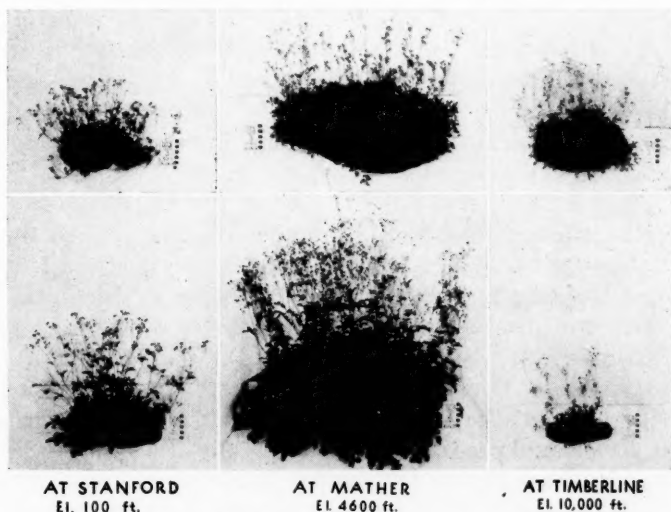


FIG. 3. *Potentilla glandulosa*: clones of the subalpine race, from 5,800 ft. altitude (lower row), and alpine race, from 10,000 ft. (upper row), both referable to ssp. *nevadensis*, showing modifications and racial differences at the three transplant stations.

The lower row of Fig. 2 is the clone of a plant representing the climatic race native in the Coast Ranges of California. This race grows well both near sea level at Stanford and at Mather at 4,600 feet, but it fails to survive at Timberline. Although it grows somewhat larger at Stanford than at Mather, it survives equally well in both environments. In its mild, native climate and in the

garden at Stanford it is in active but slow growth almost the entire year. It is sufficiently cold-resistant not to be injured by the frosts during the winters at Stanford. The more severe winters at Mather, however, force it into dormancy for some six months, thus delaying its entire seasonal development, but not interfering with its capacity to flower and produce ripe seed. Most of the plants of this species in the California Coast Ranges from 600 to 5,000 feet altitude are referable to this climatic race, for in spite of considerable individual variation, they have fundamental morphological and physiological characteristics in common by which they may be distinguished from all other races. Also, they react basically the same in the experiments regardless of the elevation of their native habitats. This climatic race is recognized taxonomically as subspecies *typica*.

In the warm, western foothills of the Sierra Nevada up to mid-altitudes, there is another regional race of the same species. The Stanford and Mather modifications of a typical plant of this race are shown in the central horizontal row of Fig. 2. Like the Coast Range race, it is unable to survive at Timberline. But unlike the representatives of that race, this plant grows taller and more vigorously at the mid-Sierran station than at Stanford. It flowers and produces seed successfully at both stations. Its leaves are susceptible to even light frosts, causing the plants to become dormant even at Stanford, with its mild winters, whereas the Coast Range race is active at this time. Consequently, at Stanford, its first spring flowers appear approximately two weeks after those of the Coast Range plants. At Mather, however, where both are forced into dormancy for approximately the same period, they flower almost together, as shown by the graph in Fig. 4.

The Sierran foothill race, known as subspecies *reflexa*, occurs from about 700 to 6,800 feet elevation, but at the higher levels it is found exclusively on the warmest slopes. Its natural populations vary considerably, but a series of morphological and reactional characteristics readily dis-

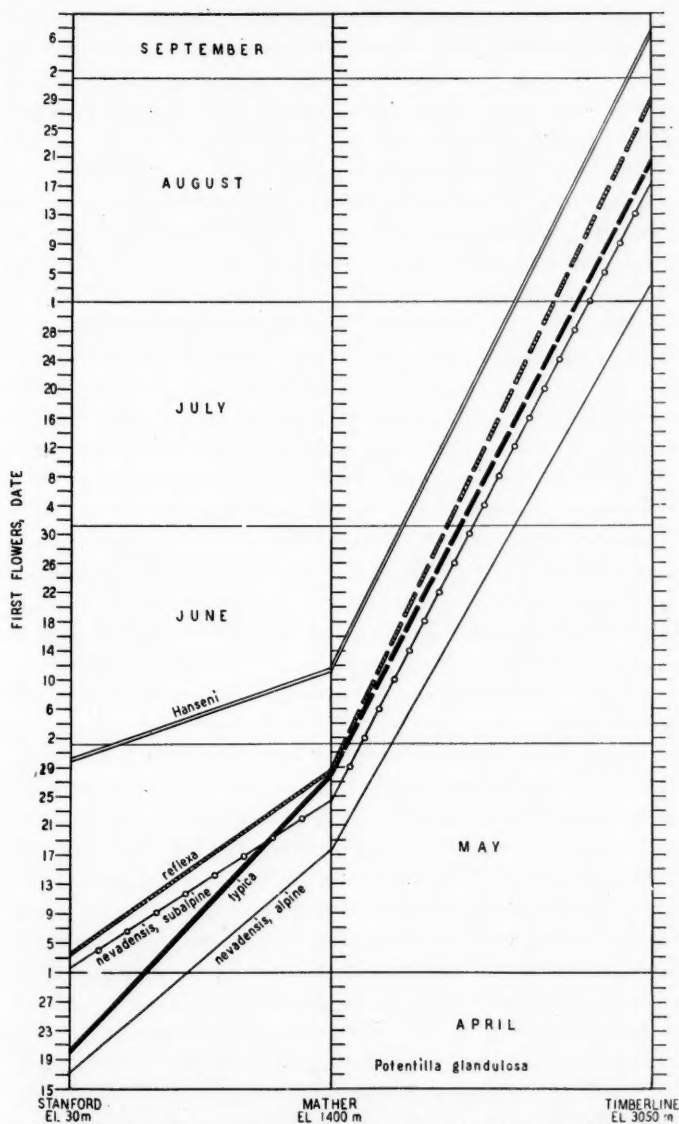


FIG. 4. Differences in dates of first flowers of climatic races of *Potentilla glandulosa* at three altitudes. Graphs represent 3-year averages of 134 clones, namely, 24 of *typica*, 47 of *reflexa*, 6 of *Hanseni*, 26 of *subalpine*, and 31 of *alpine nevadensis*.

tinguish it from the Coast Range race. Many plants from the upper altitudinal limits of its range are somewhat reduced in size, but otherwise show no unique differences in reactions at the three stations, and die equally promptly at Timberline.

In middle altitude meadows in the Sierra Nevada another race is found. It differs from the foothill race not alone in its preference for moister, cooler habitats, but in a number of other characters and in its reactions. Three modifications of this mid-Sierran meadow race are shown in the upper row of Fig. 2. It is definitely most vigorous in the mid-altitude environment. Unlike both the foothill and the Coast Range races, members of the meadow race are able to survive not only at lower elevations but also at Timberline. Although greatly reduced in size and vigor, the clone-member at Timberline has been able to withstand the rigors of the alpine climate for ten years. It produces flowering stems there, but because of the shortness of the season, it is unable to produce ripe seed. At Stanford, the meadow race tends to die out of the cultures more frequently than the foothill form. It is the most modifiable of all the races of *Potentilla glandulosa*, yet close comparison reveals the fundamental identity in structure of clone-members at the three stations.

The Sierran foothill and meadow races overlap in altitudinal distribution although the meadow race rarely descends below 4,000 feet. But a rather clear-cut ecological separation is maintained between the two, for the meadow race never grows on dry hillsides, and the foothill race very rarely invades the meadows. Hybrids between them are occasionally found near their parents on meadow borders. The meadow race is distinguished taxonomically as subspecies *Hanseni*.

Two race-complexes of *Potentilla glandulosa* are found in the Sierras above 6,000 feet. These form an intergrading series morphologically so that it is impractical to separate them taxonomically. Together they compose subspecies *nevadensis*. By their reactions, however, it

is possible to distinguish both subalpine and alpine races. This has been done, as in the other cases, by assembling a large number of individuals from a number of different habitats and elevations and observing their reactions. Representatives of these races and their modifications at the transplant stations are shown in Fig. 3. Both races survive at Timberline, but the alpine tends to be the more vigorous there. Both grow best and attain their largest size at Mather, where they are able to survive indefinitely. Neither does as well at Stanford, showing reduced stature, increased susceptibility to disease and reduced flowering, although both survive moderately well. The subalpine flowers better than the alpine at the lowland station. Both become dormant during the winter at all three stations; even at the lowland station they are dormant for two to three months.

The alpine race is one or two weeks earlier in flowering at all three stations, as shown by the graphs in Fig. 4. This difference in earliness is sufficient to permit it to produce ripe fruit consistently in the very short growing season at Timberline, whereas the subalpine plants can ripen seed only in the most favorable years. The alpine plants are so rapid in their development that, in spite of their winter-dormancy, even at Stanford they are able to flower before the Coast Range races. Moreover, the alpine plants are more frost-resistant than the subalpines, a difference which is most accentuated at Timberline. In the Sierra Nevada, plants reacting like subalpines are found at altitudes between 5,000 and 8,000 feet, and alpine-reacting types may occur between 7,500 and 11,000 feet.

Morphologically, subspecies *nevadensis*, with its subalpine and alpine races, stands out as a very distinct unit. Moreover, it is self-sterile, whereas the others are self-fertile. But the physiological differentiation within the subspecies, separating an early-flowering, dwarfish and alpine race from a later-flowering, taller, subalpine one, may be just as important as the differences distinguishing this subspecies from the others.

Close study of modifications, such as are illustrated in Figs. 2 and 4, discloses that the climatic races retain their morphological and physiological individuality in the three very different environments in spite of striking modifications in general appearance. Structural features such as habit of branching and density of inflorescences, shape, venation and general texture of leaves, character and density of pubescence, distribution of glands, presence or absence of anthocyanin in stems, size, color and shape of flowers, size and color of seeds, and similar characters serve to identify each climatic race, and even each individual. On the other hand, such characters as size of vegetative parts, number of stems and vigor of growth may be profoundly modified in different surroundings, although these also are characteristics of the various races. Moreover, the manner in which a given climatic race or individual is modified is as much a part of its character as a morphological feature. Each climatic race appears particularly adjusted to thrive in its native environment, although with competition removed, it may be even more vigorous in another environment. The entire cycle of development of each climatic race appears to be fitted to the environment in which the race is native.

Modifications resulting from exposure to changed environments are quickly reversible when plants are returned to their original environment. From these transplanting experiments there is no evidence that modifications have a durable effect on the plant, even after continuous exposure to a new environment for as long as eighteen years.

Many plant groups of different families from central California were investigated and likewise found to be composed of ecologic races. Those races from the same kind of environment often show morphologic similarities as well as parallel reactions in different environments. Such correlations point to the conclusion that we are dealing with a basic principle governing the ecological differentiation of plants. Moreover, they confirm the findings

of Turesson (1922, 1925), who found in more northern latitudes in Europe the same general type of climatic differentiation in other groups of plants.

These facts naturally lead to further inquiry as to the basis of climatic differentiation. It has been experimentally demonstrated that climatic races have a genetic basis. Their hereditary differences may be either purely genic or associated with differences in chromosome number, depending upon the evolutionary history of the forms in question. In the case of *Potentilla glandulosa*, all of the races have seven pairs of chromosomes, and no genetic barriers have been found between them. For example, the foothill and alpine races (the most unlike within the species morphologically and physiologically) hybridize without any difficulty and their hybrids are fully fertile. A large second generation has segregated nearly every conceivable recombination of both morphological and physiological traits, although there is considerable linkage, as would be expected with the low chromosome number. Nearly every morphological character was found to depend upon a small series of genes, each of minor but cumulative effect. Furthermore, traits that appear to have an adaptive value, like earliness of flowering, duration of dormancy, frost resistance, growth rate and self-fertility, segregate too, indicating a genetic basis for them as well as for the others.

We find, therefore, in *Potentilla glandulosa* a remarkable differentiation into major ecologic races fitted to occupy very contrasting environments. This differentiation depends upon a multiplicity of genes in a few chromosomes, but these genes are interchangeable without upsetting the physiological balance of the offspring. The apparent absence of genetic barriers within this group indicates that all these climatic races belong within one species.

ACHILLEA

A different pattern of regional differentiation is found in the western yarrow of the *Achillea millefolium* com-

plex. Its members have an even wider distribution than *Potentilla glandulosa*, and cover many climatic zones with different races. However, a difference in chromosome number separates the West American representatives into two large groups. Plants from mid-elevations on the west slope of the Sierra Nevada eastward across the crest of the range, the Great Basin and the Rocky Mountains have 18 pairs of chromosomes. Those west to the coast have 27 pairs. Since these differences in chromosome number impose a definite barrier to interbreeding, at least two species are involved. The coastal species is *Achillea borealis* Bong., the interior one is *A. lanulosa* Nutt., and in each there has been ecologic differentiation into races fitted to different climates.

The change in chromosome number in *Achillea* has offered no complication to the formation of climatic races across California very parallel to those found in the *Potentilla*. Some of these are illustrated in Figs. 5 and 6. The reactions of two races of *A. borealis* at the transplant stations are shown in Fig. 5. The upper row shows clone-

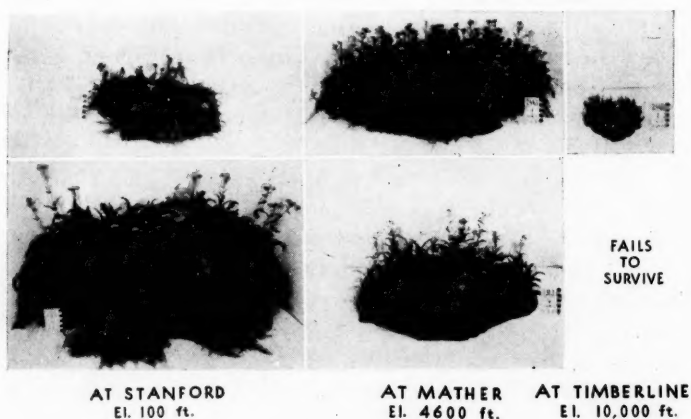


FIG. 5. Clones of two latitudinal races of *Achillea borealis* at three altitudes. Both are hexaploid, $n=27$. Above: plant from Seward, Alaska; below: plant from Berkeley, California; both from near sea level but separated by 22° of latitude.

members of a plant from coastal Alaska as they appear at the three transplant stations, while the lower row shows corresponding clone-members of a plant from the central California coast, 22 degrees of latitude farther south. The Alaskan race is able to live at all three stations and is early flowering, but its stems are very susceptible to

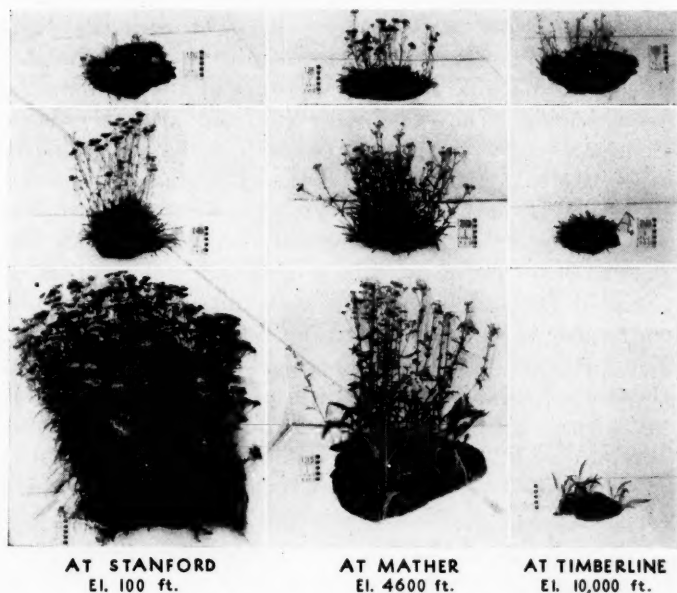


FIG. 6. Clones of three altitudinal races of *Achillea lanulosa* at three altitudes. All are tetraploid, $n=18$. Top: an alpine, from 10,700 ft. altitude; center: a subalpine, from 7,100 ft.; bottom: a mid-Sierran plant, from 4,675 ft.; all from the Sierra Nevada along the station transect.

frost and are killed at Timberline before they are able to ripen seeds. By far its best growth is attained at the mid-Sierran station. The southern race, on the other hand, cannot survive at Timberline, and it even suffers a loss of vigor at the mid-Sierran station. It grows most successfully at Stanford, near its native habitat. At both stations it is in flower a month and a half later than the Alaskan plant.

Three altitudinal races of *A. lanulosa* of the Sierra Nevada are illustrated in Fig. 6. The reactions of clone-members of a mid-Sierran individual (lower row), a subalpine (center row) and an alpine (upper row) are shown at Stanford, Mather and Timberline stations. The mid-Sierran race (from 4,675 feet) survives only two or three years at Timberline and seldom is able to develop more than a few basal leaves there. At Stanford, however, it develops even more vigorously than in its native habitat at Mather, but it is far more vigorous at Mather than the coastal form. The subalpine race, from 7,100 feet elevation, survives well at all three stations, but is unable to ripen fruit at Timberline because the stems are frost-killed before maturity, as shown in the figure. The alpine race, on the other hand, thrives at all three altitudes, but grows more vigorously at both mountain stations than at Stanford; it is early and frost-resistant enough to be able to mature in its native environment in favorable years. The most frost-resistant race (not illustrated) comes from the Great Basin, east of the Sierra Nevada. It is a fairly tall form, which remains green and active at the alpine station long after the other plants are frost-killed, but is so slow in its development there that it is unable to mature fruit.

Accordingly, in *Achillea*, as in *Potentilla glandulosa*, the regional races appear to be well adapted to their natural environments, although they do not always make their maximum growth in the climate in which they are native.

OTHER SPECIES

A summary of a survey of regional differentiation in several groups of widely distributed California plants is presented in Fig. 7. The diagrammatic profile at the top indicates the elevations in a transect across central California. The approximate distribution of regional races of various plant groups is shown below the profile and also their differences in chromosome number. It will be seen that some of the plant groups are distributed across

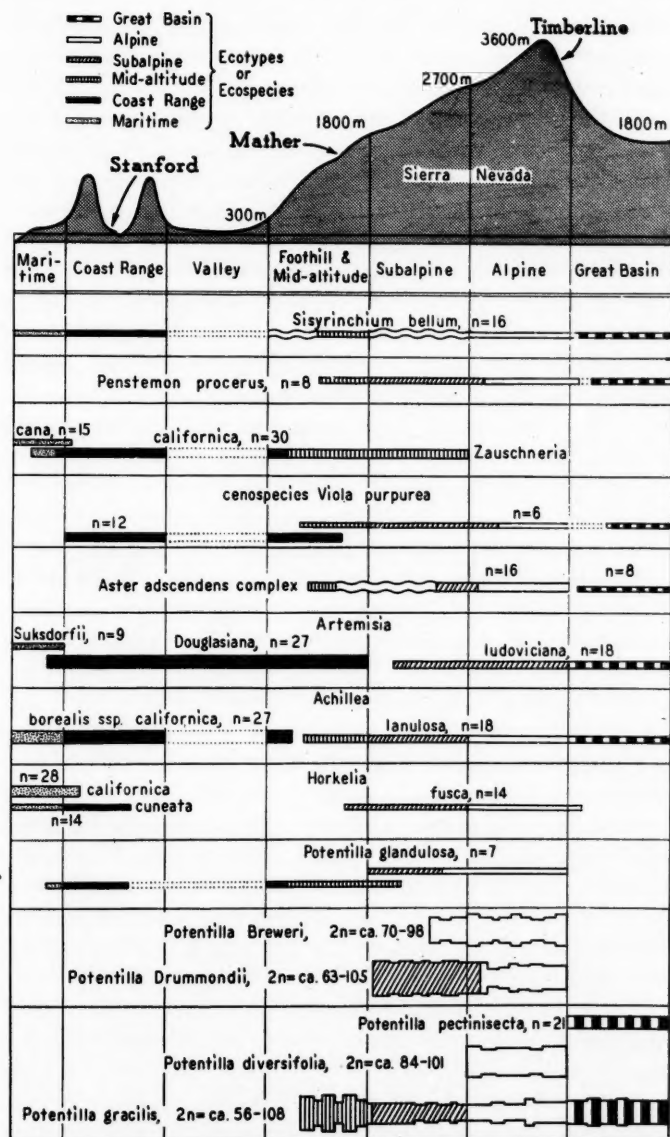


FIG. 7. Distribution of major climatic-races within species complexes in a transect across central California. The width of the symbols roughly indicate the degree of polyploidy. Further explanation in text.

the entire transect, while others occur on only a part of it. Almost all are absent from the San Joaquin Valley, an expanse populated primarily by annuals.

Of the eleven complexes shown, three have effected their differentiation without change in chromosome number, namely, *Sisyrinchium bellum*, *Potentilla glandulosa* and *Penstemon procerus*. The remainder have simple or complex differences in chromosome number within them. The *Potentilla* species of the two complexes shown at the bottom of Fig. 7 are the antithesis of *Potentilla glandulosa* cytologically. In contrast to the extreme regularity of the latter, these species present differences in chromosome number even among the individuals of one population (as suggested by the varying widths of the symbols in the graph), and all plants have many unpaired chromosomes. These groups probably reproduce asexually through apomixis. Yet despite this great variability in chromosome number and lack of pairing at meiosis, they have developed climatic races very parallel to those found in *P. glandulosa*.

In the remaining six cases in the graph the chromosome number changes somewhere along the transect. The component races of almost all these complexes are so closely related that at one time or another they have been combined in one species. However, the differences in chromosome numbers produce genetic barriers that prevent free interbreeding, and these differences are usually correlated with differences in morphology. This makes it possible to recognize the chromosomal groups as taxonomic species. Closely related species differing in chromosome number usually do not overlap very much in distribution, but replace one another in different climates.

There is no observable correlation between degree of polyploidy and environment, for in some complexes the forms with low chromosome numbers are at high altitudes, in others, at low altitudes, in some, near the sea, in others, inland. Irrespective of what the chromosome number is, however, or where it changes, each complex

has developed a series of climatic races of parallel reaction, fitted to the climates in which they are native. An exception to this rule is found in *Artemisia Douglasiana*, for no well-defined climatic race has been discovered in this species, which, nevertheless, covers a rather wide range of environments. There is some evidence that this species may be an amphidiploid of comparatively recent origin, produced by the addition of the chromosomes of the maritime *A. Suksdorfii* with those of *A. ludoviciana* from the interior mountains and desert plateaus. The combination of chromosomes from such ecologically different species should produce a form capable of inhabiting a wide variety of environments.

CONCLUSIONS

This survey and the one conducted by Turesson in Europe indicate that the genetic-physiologic differentiation of a plant group is correlated with the climatic zones it occupies. This follows from the fact that the same kinds of environments are occupied by races that have similar patterns of reaction, even though they belong to unrelated genera or families. This is found to hold irrespective of whether or not the regional forms differ in chromosome number.

The usual pattern of differentiation is purely genetic, with relatively few major steps involved; but superimposed upon this one often finds a cytological differentiation, with one or two changes in chromosome number across the California transect. However, the effects of increases in chromosome number must have been far overshadowed by the selective influence of the environment in determining the appearance and reactions of plants. From these considerations it appears that it is the genes in the chromosomes, and not the number of chromosomes, which determine the climatic adaptation.

From the point of view of fitness to the environment it is evident that the ecologically important unit is not the species, but the regional climatic race, or, to adopt Tures-

son's term, the *ecotype*. Several of these may combine to form a species, or a single ecotype may develop an isolating genetic barrier to form a monotypic species, such as *Zauschneria cana*, *Artemisia Suksdorfii* and *Horkelia californica*, in Fig. 7. Such monotypic species occupy a narrow climatic belt and show little variation and adaptability. However, it makes little difference whether a given area is populated by a series of ecotypes belonging to one species, or by a series of monotypic species belonging to one species complex, or by a combination of both. The evolutionary past and future differ, however, in the three instances.

Evolutionary processes have left plants arranged in groups of various order and separation, such as populations, ecotypes, species and species complexes. These groups indicate stages in evolutionary differentiation, and they have evolved only where there is a diversity of environments.

There are many mechanisms by which living things can increase their hereditary variation, but regional differentiation requires the discriminating selection offered by unlike environments. We have no evidence that the direct influence of environment produces fundamental hereditary changes in species, but major alterations in environments provide new habitats and refuges for the products of nature's continual experimentation among all the plant species that populate a given area.

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PROBLEMS OF INSECT SPECIATION IN THE HAWAIIAN ISLANDS

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DURING the past century a great many supposedly distinct explanations have been proposed for the phenomenon which we know as organic evolution. Fortunately, it is now generally recognized that not one but a large number of factors influence the formation of new species. However, it becomes apparent that one evolutionary process may dominate the picture in one spot or at one time while others may be critical at other times or places. Perhaps the greatest desideratum in the study of evolution to-day is the sifting out of these fundamental processes. Each new and particularly striking example of some old and well-known phenomenon may then serve to focus attention on essentials and to further crystallize our ideas regarding the origin of species. In the present discussion insular evolution will be stressed, not because it is representative of evolution as a whole but simply because it illustrates clearly a type of evolution wherein isolation plays a dominant role with competition reduced to a minimum.

Biologically, the truly oceanic islands differ strikingly from mainland areas and from the so-called continental islands which cling to the continental shelves. Completely isolated since their volcanic peaks first arose above the surface, these islands have supported an independent biota for a long period. Hence the traditional picture of a tropical paradise is not without its biological significance for insects as well as for man, the human beach-comber having a counterpart in the decadent endemic plants and animals of the islands.

Most isolated of all the large oceanic islands, the Hawaiian Islands stand as the epitome of insular isolation. Modern advertising has extolled the beauty of

Waikiki, has made much of the pineapple and sugar-cane, but remains silent concerning the 80 per cent. endemism of the Hawaiian biota. With practically no native mammals, reptiles or amphibians and without any representatives of such commonplace insect orders as the mayflies, stoneflies and caddis flies and such common coleopterous families as the leaf beetles, lamellicorn beetles, stag beetles and many others, the Hawaiian Islands stand to-day as the most unique biological area in the world. Here the land birds have nearly all evolved from a single introduction and now form the distinctive family Drepaniidae with nearly forty species. Even more remarkable are the various groups of land snails with nearly five hundred distinguishable forms. These belong to three endemic families, the Achatinellidae, Leptachatiniidae and Amastridae, with no close relatives known from elsewhere, even in other islands of the Pacific.

This same phenomenon of inordinate proliferation of species is seen in so many groups of Hawaiian insects that it has become the rule rather than the exception and we look for a reason when we encounter a group which has not evolved through insular isolation. These latter cases may usually be classed as recent immigrants, having arrived presumably since the first outrigger canoes of the Polynesians. Such relatively recent arrivals have replaced the native biota, particularly in the lowlands, and have quickly spread to all the islands. Apparently they have not yet had sufficient time to lose the adaptability and powers of dispersal which enabled them to reach these remote islands and become established there. Hence they are able to keep their various semi-isolated populations within the fold. More perplexing are the monotypic endemic genera. Wood-boring beetles of the genus *Parandra* may be taken as an example of this type of Hawaiian insect. The species of *Parandra* are widespread over the world, each major zoogeographical region having a distinct species. Moreover, the group is the most primitive of the entire family Cerambycidae. That

Parandra has not fostered a large branch of the genus while evolving into such a distinct form in Hawaii suggests that it was already old and stereotyped when it arrived or that it was sufficiently adaptable to live as a single form under a variety of conditions. In either case it seems obvious that the phylogenetic history of this group profoundly influenced its possibilities for future evolution.

Of greatest interest, however, are the large groups of closely related species which have evolved in the Hawaiian Islands. The *Proterhinus* weevils with one hundred and fifty species, Cerambycids of the genera *Plagithmysus* and *Neoclytarus*, Lygaeid bugs of the genera *Nysius*, *Neseis* and *Oceanides* in the tribe Orsillini and a host of other genera in all the principal orders of Hawaiian insects, have developed unique branches of from six to over one hundred species. Each of these is a small phylogenetic world in itself. Here we find geographical replacement well developed with distinct forms on each separate island and often on each host. The distribution is so abruptly discontinuous that it is difficult to say at what point during divergence two forms become subspecies or species as the case may be. Very unfortunately the taxonomic details have not been correlated with geographical and host distribution in most groups of Hawaiian insects. Hence any specific evolutionary remarks in the following pages will deal with but a single group, the Orsillini, which I have recently studied in the hope that it may eventually be suitable for more precise evolutionary study of cross-breeding and of variation in natural and laboratory populations.

In analyzing the present problem it will first be necessary to review briefly the facts and theories concerning the origin and history of the islands, their physical and biotic characteristics and such special characteristics of the individual faunistic and floral elements as may have contributed to their present remarkable degree of development.

CHARACTERISTICS OF THE ENVIRONMENT

Origin: The Hawaiian archipelago is clearly volcanic in origin with subsequent or coincident coral formation in some areas. Some geologists maintain that the islands are as recent as Pliocene or even Pleistocene, having arisen as volcanic cones from the bottom of this deep portion of the great Pacific basin. In contrast to this orthodox view, Gregory (1930) speaking as a Geologist and Pilsbry (1916) and Campbell (1933) in dealing with the land shells and plants, respectively, advocate a tremendous Pacific continent or at least land connections to the southeast. Furthermore, a Cretaceous origin has been postulated, largely on the basis of the known age of the nearest mainland relatives of the peculiar families of land shells. Speculating on the basis of comparative rates of evolution in widely separated regions is dangerous, but it does seem obvious that the peculiar genera or even higher groups of insects of Hawaii are very old.

This is obviously not the place to settle such moot questions, although some sort of rational story is necessary if we are ultimately to trace the history of the Hawaiian Orsillini. For our purposes, the minority opinion of the "Pacific continent" advocates is discarded because it raises more problems than it solves. In lieu of this the "stepping stone" hypothesis is adopted. According to this view migration takes place by short jumps from island to island along the chains or arcs which run in a northwest-southeast direction across portions of the Pacific basin. Geologically these arcs have been likened to "ripples on the ocean floor" by DuToit (1937) and were termed the "Oceanides" by Suess (1909), who visualized them as "advance waves" of continents migrating from the southwest. Whether continents have actually migrated or not, recognition of the arcs as lines of crustal weakness is an illuminating explanation for this characteristic feature of the Pacific basin. That many such island chains might have come and gone during the history of the Pacific is suggested by the number of isolated

shoals and reefs, scarcely awash, which are scattered here and there over the ocean and are surrounded by depths of nearly fifteen thousand feet in some instances. Along such chains during periods of elevation, inter-island communication must have taken place with much greater frequency than the traditional blowing of insect waifs and strays across thousands of miles of open ocean.

As has often been pointed out, the main Hawaiian Islands form a more or less orderly progression in point of age. East Hawaii is youngest with active volcanoes at the present time, while West Hawaii (Kohala Mountains) is much older. East Maui with the now extinct but little altered crater of Haleakala is relatively recent as compared to west Maui. The chain continues through Molo-kai to the Koolau Range of Oahu which is thought to be younger than the western Waianae Range. Finally Kauai, the most isolated of the entire group and situated at the extreme northwest of the chain, is the oldest of the main islands.

To the northwest the extensive chain of Leeward Islands extends through twenty degrees of longitude and about eight degrees of latitude. These leeward islands decrease progressively in elevation and change from volcanic rock to coral towards the northwest. Hence geologists have concluded that these islands were at one time high and eventually, by either subsidence or weathering, were reduced to their present respective levels. Subsequent coral formation and fluctuations in sea level have resulted in the coral islands or reefs of the present day. The only present-day evidence of the existence of an early Leeward Island biota is a small endemic element consisting of a few birds, plants and insects on Nihoa, Laysan and some of the other islands, and an endemic *Rhyncogonus* weevil extending as far as remote Wake Island. However, the Leeward Islands, as well as the Micronesian Islands, show evidence of tremendous change; Guam, for example, being capped in great part with limestone, so that their ancient biotas, if any, would

certainly have been wiped out, perhaps completely. The present fauna, then, must have arrived relatively recently from neighboring land areas, and we actually find that, but for the few endemics mentioned above, the fauna consists of wide-spread immigrants characteristic of all the coral islands of the Pacific.

It is the ancient leeward chain of high islands, however, which is of importance as a migration lane for the endemic Hawaiian biota. Such a circuitous route would eventually link Hawaii by way of former Micronesian islands, with New Guinea and all its interrelated or once-connected regions such as Australia, New Caledonia and New Zealand and thence, perhaps, to Antarctica and around to Juan Fernandez. The truly oceanic south and central Polynesian islands were doubtless populated in a similar fashion along chains of islands and from the same original source but, as suggested by most students of the problem, along different and more direct routes via Fiji, Samoa, the Tuamotus, the Austral Islands and other stepping stones or island chains. This accounts for the similarity between the animal and plant groups of Hawaii and those of Australia, New Zealand, Juan Fernandez, etc., through community of origin, yet provides a reasonable explanation for the complete absence of many groups, such as the Orsillini, from southern Polynesia—the very islands where they would be expected to occur, had the fauna of Hawaii been derived directly from the southwest.

Physical Conditions: On the main islands of the Hawaiian group a great variety of physical conditions is to be found; elevations from sea level to almost fourteen thousand feet; temperatures from 85° or 90° F. in the lowlands to well below freezing on the top of Mauna Kea, which is snow-capped in the winter and bears unmistakable moraines and striae of glaciers; yearly rainfall from less than twenty inches to more than five hundred inches on Mt. Waialeale; edaphic conditions ranging from limestone so recent and hard that it clinks under foot, through

equally hard, smooth "pahoehoe" lava or unbelievably rough "a-a" lava, to the very rich humus of the rain forest floor and finally to the bog swamps on the high plateaus of Maui, Oahu and Kauai; and wind conditions varying from the northeast slopes which are constantly exposed to the trade winds to the stifled heads and pockets of valleys on the leeward sides of the islands.

Despite the great variety over the islands as a whole, there is a remarkable uniformity of conditions in any particular repeated ecological niche. So great is this uniformity that identical physical conditions, for all practical purposes, can be found, with only a few exceptions, in particular spots on all the main islands.

Biotic Conditions: On oceanic islands biotic conditions are in some respects more important than physical conditions in directing the course of evolution of specific groups. This is due to the depauperate nature of such regions, a condition which Gulick (1932) has termed "disharmonic" because many entire groups of plants and animals are entirely absent, never having reached such remote shores. However, an apparently harmonic condition has developed, at least in the very old Hawaiian Islands, because such plants and animals as are present have had sufficient time to thoroughly occupy all available ecological niches, thus forming hierarchical microcosms. This is particularly true of the plants, whereas animals are very scarce in some habitats such as fresh water streams, the soil, and many plants. Competition in some of these latter situations is reduced to a minimum, so that an immigrant insect suited to the local conditions ought to be able to live and breed uninterruptedly. Apparently, however, such species eventually become decadent under these conditions because new immigrants from highly competitive mainland areas, when accidentally or purposely introduced into oceanic islands by man, are found to displace the insular forms.

A tremendous biological upset has occurred in the lowlands of most oceanic islands. In the Hawaiian Islands

there is good reason to believe that the entire area from sea level up to an elevation of approximately two thousand feet was covered at one time with a rich, endemic, lowland forest. To-day the region supports very little except immigrant species which have run wild, and cultivated crops. At least part of this change resulted from accidental and deliberate introductions of plants by the Polynesians and from the fires and clearing operations coincident with their occupation of the islands. By far the greatest destruction, however, has been by the white man, in connection with his cultivation and introduction of domesticated animals. As a consequence the original flora has been wiped out almost completely, only a few patches of lowland forest remaining, such as that on Lanai, protected for some years by Mr. George Munroe. Some lowland plants reported by early explorers, and even some described by Hillebrand as late as 1888, are now gone. Even in places where a few endemic plants still persist in the lowlands, the endemic fauna has largely disappeared and is replaced by immigrant species. Of the latter, by far the worst is the predaceous ant, *Pheidole megacephala* (Fabr.), which has killed off almost all native insects of the lowlands. A few species of native bees and wasps have persisted, and a number of native Heteroptera (including *Nysius*) and Homoptera actually manage to thrive there. These resistant natives may, however, be relatively recent immigrants in the sense of geologic time, as they belong to widespread genera which have not yet lost their ability to compete with foreign invaders.

CHARACTERISTICS OF THE INSECTS

There are certain characteristics of the insects of Hawaii which would appear to make them particularly likely to succeed in island colonization. Thus the weevils, characteristic of the faunas of all islands, are usually small bark dwellers with secretive habits. Equally characteristic of most islands are members of the genus *Nysius*. These insects are small with a large ratio of surface to

volume and hence are easily blown for considerable distances. Relying upon strong flight as well as wind are the milkweed butterflies and the large dragonflies of the genus *Anax*. Obviously these insects need to be unusually adaptable and able to withstand the adverse conditions of wind or oceanic travel in addition to possessing mechanical means of transport.

EVOLUTION

Having reviewed the facts essential to the problem, it may now be profitable to explore the various possibilities in the evolution of one of the largest and most diverse groups of Hawaiian insects, the Orsillini. This is a particularly favorable example because it is polyphyletic, its various branches exhibiting the features of the decadent endemic genera as well as of the modern dominant type belonging to worldwide genera. Thus the species of *Oceanides* and *Neseis* are restricted to particular islands and host plants in the native forests above two thousand feet. Moreover, phylogenetic groups within these genera are intimately associated with particular families or closely allied groups of plants. In contrast to this, species of the nearly cosmopolitan genus *Nysius* are mostly wide-spread in the Hawaiian archipelago and occur on a variety of plants such as introduced weeds or modern groups of endemic plants.

The endemic genera *Oceanides* and *Neseis* probably migrated down the long series of Leeward Islands before the main islands of the present day were built. They must have started not later than earliest tertiary times as judged by mainland evolutionary rates or perhaps later than this considering that evolution has taken place in the absence of severe competition. It is difficult to say whether a single stock similar to present-day *Nysius* started along the chain, evolving the very special and peculiar characteristics common to these genera, or whether one or two representatives of a then wide-spread type set out and were subsequently replaced in mainland

areas by the now dominant genus *Nysius*. In any event, at the same time or while the islands near the continent were still high, typical *Nysius* of several types also started the long and precarious journey. Still later, during the relatively recent past, modern *Nysius*, which differ only in trivial details from mainland forms, migrated and, indeed, are still migrating along the low coral islands of the present-day Leeward Chain.

The early members of the *Neseis* stock doubtless preferred endemic plants of the family Urticaceae or, if catholic in their tastes, must subsequently have become restricted in great part to this group of plants. Similarly, the *Oceanides* stock became attached to rubiaceous and euphorbiaceous plants and a few others of this general type.

Now with insular isolation and marked host preferences the stage was set for speciation. A considerable mutation pressure was greatly increased in effectiveness by low environmental resistance. At the same time and opposed to mutation pressure the effect of the scattering of variability during reproduction, with its tendency towards homozygosity (Dobzhansky, 1937, and Wright, 1931 and 1932) was avoided by the unusual degree of isolation. Small populations, such as would start with a single gravid female blown to a neighboring island, would build up entirely apart from the parent population. Under such circumstances Wright has shown that particular genes will tend, merely by chance, to become either fixed or lost. This is in marked contrast to the equilibrium of variability maintained in very large populations.

Given a large number of isolated populations, so derived, there would follow mutations of varying magnitude which eventually must have included physiological isolating mechanisms, because we now find species such as *nitidus* and *hiloensis*, obviously monophyletic, coexisting and yet maintaining their distinctness. In this manner island after island was and possibly still is being populated by the various types of *Neseis* and *Oceanides*. Sec-

ondarily, and apparently after the present islands of the main group were formed and isolated, certain of these species, notably *nitidus*, *hiloensis* and the *mauiensis* group, broke up. This may have occurred either by the break-up of a single population which occurred on all the islands or by migration from island to island. The latter alternative appears more plausible, because *hiloensis* never reached Kauai, although it occurs in company with *nitidus* on each of the other islands. The species then proceeded to diverge, and have now reached varying degrees of differentiation, the extent of which can not be determined without breeding experiments. Thus the various species in the endemic genera fall into a series, ranging from (1) the wide-spread and variable *Oceanides nimbatus* Kirk., not yet broken up into distinguishable forms on the various islands, through (2) the scarcely differentiated *Neseis saundersianus* Kirk. to (3) the "polytypic species" (Huxley, 1938) or "Rassenkreis" (Rensch, 1929) *Neseis nitidus* White, which has structurally distinct but closely allied races on each island, then to (4) the "supra-species" (Huxley, 1938) *Neseis hiloensis* Perkins, the Oahu form of which was unhesitatingly called a distinct species, until a connecting link was discovered on Molokai, and finally to (5) that which Huxley (1938) has called a "geographical subgenus" and Rensch (1929) has called an "Artenkreis," namely, the *Neseis mauiensis* Blackburn group which has diverged to such an extent that the Oahu and Kauai forms have attained the status of full species and had not even been recognized as belonging to this group previously.

The cosmopolitan genus *Nysius*, s. str., is represented by a greater variety of forms in Hawaii than in any equivalent area elsewhere in the world. Moreover, some of the species are the most divergent known anywhere. As mentioned above, this genus may have left its mainland allies at a later date than the endemic genera discussed above. In any event, it seems likely that its representatives arrived at the present high islands at

different times because the species vary in their characteristics from entirely unique species to species that differ from mainland species only in trivial details. When the various species of *Nysius* arrived they evidently favored modern groups of plants such as the Compositae, Poaceae and Portulacaceae, upon which their congeners are found throughout the world. This is inferred from the fact that they occur on native members of these families in Hawaii to-day. Each species must have built up enormously in numbers and, in most cases, acquired a greater range of variability through increased survival of mutant forms and partial isolation. Most of them remained as single species due to their inherent ability to travel from island to island. The group as a whole, due to its adaptability, soon invaded the entire archipelago from sea level to the mountain tops, the various forms being able to compete with both the decadent endemics and such introduced forms as already inhabited these regions. A few species of *Nysius* became truly localized on particular islands and plants, but most of them remained tolerant in such matters, although showing marked host preferences. The most recent invader, a new species, is even now moving slowly down the Leeward chain, where it exhibits bewildering variation.

Finally man arrived with a variety of lowland plants and animals which, together with fire and the plow, annihilated most of the native fauna and flora below two thousand feet. *Neseis* and *Oceanides* retreated from or died out in the lowlands, and are now making a last stand in the highlands, with many other relics. Not so with *Nysius*, however; still sufficiently adaptable, the bugs of this genus continue to thrive throughout their entire range, having withstood all newcomers, including the predatory ants. As their native plant hosts disappeared or were replaced by weeds in the lowlands, these bugs turned to new hosts which, in cases such as *Erigeron*, must be very similar to their original host plants before they invaded the islands. Fortunately, only *nemorivagus*

White, of all these species, has thus far turned to cultivated crops. This is particularly noteworthy in view of the notorious pests belonging to this genus elsewhere in the world.

The conclusion seems inevitable, then, that either geographical isolation or host isolation, or both, is sufficient to set the processes of species formation in operation, while the biotic environment plays an all-important rôle in determining the rate and limits of this evolution. A disharmonic insular area with great gaps in its environment allows many non-lethal mutations to persist, whereas a fiercely competitive mainland environment rigidly rejects all but the best adapted, thus favoring adaptive evolution by natural selection.

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ON JUDGING THE SIGNIFICANCE OF A DIFFERENCE OBTAINED BY AVERAGING ESSENTIALLY DIFFERENT SERIES

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IN genetic experiments, as well as elsewhere, the need often arises for comparing the frequencies of events of a given kind (*e.g.*, mutations) under two different conditions, *A* and *B*, when the observations have been made in the form of several different series of data, series 1, 2, 3, etc., to *k*, under both conditions, in such a way that lots 1*A* and 1*B* correspond with one another, 2*A* and 2*B*, 3*A* and 3*B*, etc., as shown in Table 1. It is understood that the conditions may vary from series to series as well as between the two lots, *A* and *B*, of any one series, but that, aside from the effects of random sampling, the two lots of a given series differ from one another only with respect to the special pair of conditions under investigation. We will further suppose that the number of observations varies in a more or less irregular way from series to series as well as between lots *A* and *B* of a given series, so that, for example, the total number observed in lot 1*A* might be larger than in 1*B*, but in 2*A* smaller than in 2*B*. For each lot, in each series, the number of events of the given kind, *i.e.*, the "successes," as well as the total number of observations is recorded; we may call this absolute number of successes *P*, and the lot to which this number pertains may be designated by a subscript, P_{1A} thus being the number of "successes" in series 1 under condition *A*. By the same method of representation n_{1A} would represent the total number observed in series 1 under condition *A*, and the absolute number P_{1A} divided by n_{1A} would be the frequency or proportion of the "successes" in the lot in question (1*A*), and may be represented by p_{1A} . The question now is to find the most representative average values of p_A and of p_B , based on all the series together,

TABLE I

ILLUSTRATION OF THE METHOD OF AVERAGING HERE DISCUSSED. (EACH SQUARE OF "DATA" GIVES ABOVE THE ALGEBRAIC DESIGNATION OF THE TERM, AND BELOW A NUMERICAL EXAMPLE FROM AN EXPERIMENT TO DETERMINE THE EFFECT OF TEMPERATURE ON THE PRODUCTION OF MUTATIONS BY X-RAYS, AFTER MAKHLJANI AND MULLER)

Number of series	Lot A			Lot B			A and B combined			Weight of series n_h $\left(\frac{2n_A n_B}{n_A + n_B}\right)$	Weighted values		
	Total number observed	Absolute no. of "events"	Proportion of events p_A $(=P_A/n_A)$	Total number observed	Absolute no. of "events"	Proportion of events p_B $(=P_B/n_B)$	p		q $(=1-p)$		Weighted frequencies for A $(n_h p_A)$ $(=P_{hA})$	Weighted frequencies for B $(n_h p_B)$ $(=P_{hB})$	Error ² of the difference $P_{hA} - P_{hB}$ $(=2n_h p q)$ $= (n_h e_d)^2$
							$\left\{ = \frac{P_A + P_B}{n_A + n_B} \right\}$						
1	n_{1A} 1018	P_{1A} 63	p_{1A} .062	n_{1B} 748	P_{1B} 44	p_{1B} .059	p_1 .061	q_1 .939	n_{h1} 862	P_{h1A} 53.06	P_{h1B} 50.71	$n_{h1} e_{d1}$ 98.2	
2	n_{2A} 848	P_{2A} 40	p_{2A} .048	n_{2B} 678	P_{2B} 38	p_{2B} .056	p_2 .051	q_2 .949	n_{h2} 754	P_{h2A} 35.57	P_{h2B} 42.20	$n_{h2} e_{d2}$ 73.1	
3	n_{3A} 592	P_{3A} 31	p_{3A} .052	n_{3B} 610	P_{3B} 48	p_{3B} .079	p_3 .066	q_3 .934	n_{h3} 601	P_{h3A} 31.49	P_{h3B} 47.29	$n_{h3} e_{d3}$ 73.8	
4	n_{4A} 174	P_{4A} 7	p_{4A} .040	n_{4B} 152	P_{4B} 4	p_{4B} .026	p_4 .034	q_4 .966	n_{h4} 162	P_{h4A} 6.52	P_{h4B} 4.27	$n_{h4} e_{d4}$ 10.6	
k^*	n_{kA} 764	P_{kA} 54	p_{kA} .071	n_{kB} 640	P_{kB} 44	p_{kB} .069	p_k .070	q_k .930	n_{hk} 697	P_{hkA} 49.24	P_{hkB} 47.92	$n_{hk} e_{dk}$ 90.5	
									$\Sigma_1^k (n_{hi})$ 3076	$\Sigma_1^k (P_{hA})$ 175.88	$\Sigma_1^k (P_{hB})$ 192.39	$\Sigma_1^k (2n_{hi} p_i q_i)$ 346.2	

* In the given numerical illustration, $k=5$.

$$\bar{p}_A = \frac{175.88}{3076} = .0570; \bar{p}_B = \frac{192.39}{3076} = .0627; \bar{d} = .0570 - .0627 = -.0057.$$

$$e_d^2 = \frac{\sqrt{346.2}}{3076} = .0060. \quad \frac{d}{e_d^2} (= \chi) = \frac{-.0057}{.0060} = -.95, \text{ chance of so high a value of } \chi \text{ (i.e., chance of so bad an agreement if the differences between } p_A \text{ and } p_B \text{ were random)} = .34.$$

for comparison of these averages, " \bar{p}_A " and " \bar{p}_B ," with one another, and, secondly, to find the standard error of \bar{a} , the difference between the values \bar{p}_A and \bar{p}_B .

Ordinary unweighted averages of the p_A 's and of the p_B 's, respectively, would not give sufficient representation to the series based on larger numbers. On the other hand, the simple summation of the values of P and of n in all the series, for the obtaining of $\Sigma P_A / \Sigma n_A$ and of $\Sigma P_B / \Sigma n_B$, would result in inaccuracy caused by the fact that in this case a given series, in which as a whole the frequency might tend to deviate determinately in a given direction, participates to a different degree in the formation of the average value for condition A than in that for condition B . For the end in view, therefore, it is desirable to obtain *weighted* averages of the values p_{1A} , p_{2A} . . . p_{kA} , and of p_{1B} , p_{2B} . . . p_{kB} , respectively, using the same weight for p_{1A} as for p_{1B} , for p_{2A} as for p_{2B} , etc., that is, for the two lots (got under the two conditions) of any given series. The weight used for any given series should of course correspond to the reliability of that series as a whole, for the comparison of the frequencies, *e.g.*, p_{1A} and p_{1B} , of its two lots with one another.

The weight to be used turns out to be the so-called "*harmonic*" mean, n_h , of the numbers of observations, n_A and n_B , respectively, in the two lots of each series. The harmonic mean of the numbers in any series may be obtained by getting the arithmetic mean, not of the numbers themselves but of their reciprocals, and then taking the reciprocal of this result. Thus, in the present case,

$$n_{h1} = \frac{1}{\frac{1}{n_{1A}} + \frac{1}{n_{1B}}}; \text{ this reduces to } n_{h1} = \frac{2n_{1A}n_{1B}}{n_{1A} + n_{1B}}$$

The reason for the use of the harmonic mean in this case is as follows. If both lots alike of a given series, *e.g.*, series 1, had had the harmonic mean, n_{1h} , instead of the two different values, n_{1A} and n_{1B} , as their total number of observations, and if the same value of p were assumed to

be the true value for both lots as that p which had actually been observed in the two lots taken together (namely, $\frac{P_{1A} + P_{1B}}{n_{1A} + n_{1B}}$, which we shall call p_1), then the difference between the frequencies to be found in these two lots each having the total n_{k1} would be subject to the same error of sampling as the difference occurring in the case that was actually observed (still supposing the observed p_1 to represent the true value of p). In other words, these weights do represent correctly the reliability of each series for a comparison of p_A and p_B . And the averages thus found— \bar{p}_A and \bar{p}_B —will accordingly be such that their difference, \bar{d} , as well as their quotient, will tend to have a lower standard error, in proportion to the latter values themselves, than averages obtained by any other method.

When the above system of weighting is followed, the weighted average values \bar{p}_A and \bar{p}_B are obtained by the formulae

$$\bar{p}_A = \frac{\sum_1^k (n_{k1} p_{1A})}{\sum_1^k (n_{k1})} \quad \text{and} \quad \bar{p}_B = \frac{\sum_1^k (n_{k1} p_{1B})}{\sum_1^k (n_{k1})}. \quad (1)$$

(In making these summations and those to follow, values of n_k , p_A , etc., applying to the same series are of course taken together, thus: $n_{k1} p_{1A} + n_{k2} p_{2A} + \dots + n_{kk} p_{kA}$.) It is the difference, \bar{d} , between these weighted averages which tends to have a minimal standard error, relative to its own value. The formula for this error, $e_{\bar{d}}$, is, as shown below:

$$e_{\bar{d}} = \frac{\sqrt{\sum_1^k (2n_{k1} p_1 q_1)}}{\sum_1^k (n_{k1})}, \quad (2)$$

where, as usual, $q_1 = 1 - p_1$. Where q is very nearly 1 throughout we may neglect it, and use the approximation

$$e_{\bar{d}} \approx \frac{\sqrt{\sum_1^k (2n_{k1} p_1)}}{\sum_1^k (n_{k1})}. \quad (2a)$$

Where q , though not equatable to 1, is always rather near it, with variations that are unimportant in the final result, we may use the approximation

$$e_d^{\text{ca}} = \frac{\sqrt{[\sum_1^k (2n_{h1}p_1)]\bar{q}}}{\sum_1^k (n_{h1})}; \quad (2b)$$

here $\bar{q} = 1 - \frac{\sum_1^k (P_1)}{\sum_1^k (n_1)}$, where $P_1 = P_{1A} + P_{1B}$.

The proof of formula (2), for the standard error of the difference between the weighted average frequencies, is as follows:

$$\bar{d} = \bar{p}_A - \bar{p}_B = \frac{\sum_1^k (n_{h1}p_{1A})}{\sum_1^k (n_{h1})} - \frac{\sum_1^k (n_{h1}p_{1B})}{\sum_1^k (n_{h1})}. \quad \text{This reduces to}$$

$$\bar{d} = \frac{\sum_1^k (n_{h1}[p_{1A} - p_{1B}])}{\sum_1^k (n_{h1})} = \frac{\sum_1^k (n_{h1}d_1)}{\sum_1^k (n_{h1})}; \quad (3)$$

here d_1 is taken to represent $p_{1A} - p_{1B}$. Now the standard error of $n_{h1}d_1$ is of course $n_{h1}e_{d1}$ (where e_{d1} is the standard error of d_1), and so the standard error of $\sum_1^k (n_{h1}d_1)$ (i.e., of $n_{h1}d_1 + n_{h2}d_2 + \dots + n_{hk}d_k$) must, by the rule for the standard error of a sum, have the value

$\sqrt{(n_{h1}e_{d1})^2 + (n_{h2}e_{d2})^2 + \dots + (n_{hk}e_{dk})^2}$, that is,
 $\sqrt{\sum_1^k (n_{h1}^2 e_{d1}^2)}$. This being the error for the numerator, $\sum_1^k (n_{h1}d_1)$, of the last expression in formula (3), the error for the whole expression, $\frac{\sum_1^k (n_{h1}d_1)}{\sum_1^k (n_{h1})}$ (i.e., for \bar{d} itself),

must be

$$\frac{\sqrt{\sum_1^k (n_{h1}^2 e_{d1}^2)}}{\sum_1^k (n_{h1})} = e_{\bar{d}}. \quad (4)$$

Now e_{d1} , the standard error of the difference, d_1 , between the frequencies p_{1A} and p_{1B} , respectively, found in the two lots of a given series, 1, assuming the same true value, p_1 , is, according to the usual formula for the standard error of a difference in frequency,

$$e_{d1} = \sqrt{\frac{p_1q_1}{n_{1A}} + \frac{p_1q_1}{n_{1B}}}. \quad (5)$$

Expanding this, we have, for any given series,

$$e_{d1} = \sqrt{\frac{(n_{1A} + n_{1B})p_1q_1}{n_{1A}n_{1B}}}, \quad \text{and this in turn reduces to}$$

$\sqrt{\frac{2p_1q_1}{n_{h1}}}$. (6) Substituting the latter value of e_{d1} for the term e_{d1} in formula (4), we have, finally,

$$\frac{\sqrt{\sum_1^k(2n_{h1}p_1q_1)}}{\sum_1^k(n_{h1})} = e_{\bar{d}} \quad (2)$$

It is to be noted that when this system of averaging is used the values of n_h , of $n_h p_A$ and $n_h p_B$ (designated as P_{hA} and P_{hB} in Table I) and of $n_h p_A - n_h p_B$ (which may be denoted D_h) may be treated in the same way as if they represented the absolute numbers actually observed, when the two weighted averages and the difference between them are calculated. On the other hand, in the calculation of the errors of this difference, the values used like absolute numbers observed are now the values of n_h and of $n_h p_1$. It should be noted here that the latter value, $n_h p_1$, is not derivable from $n_h p_A + n_h p_B$.

The evaluation of the chance that a difference as great as the \bar{d} actually obtained would have occurred if the difference between the conditions *A* and *B* had been without influence on the result is of course made by looking up the probability corresponding to the value of the quotient $\frac{\bar{d}}{e_{\bar{d}}}$, otherwise known as χ . Now this quotient

need not be calculated by first obtaining \bar{d} , by formula (3), and $e_{\bar{d}}$, by formula (2), and then dividing the former by the latter, for in the division of the first expression by the second the term $\sum_1^k(n_{h1})$, present in both, cancels out, so that we are, finally, left with the simplification

$$\chi = \frac{\bar{d}}{e_{\bar{d}}} = \frac{\sum_1^k P_{h1A} - \sum_1^k P_{h1B}}{\sum_1^k(2n_{h1}p_1q_1)} \text{ or } \frac{\sum_1^k(D_{h1})}{\sum_1^k(2n_{h1}p_1q_1)}. \quad (7)$$

It is this χ which, on the average, has a maximum value, in comparison with the χ applying to the difference obtained on any other system of averaging, in cases where the difference in conditions *A* and *B* has no real influence on the results. Correspondingly, the probability for this χ has, as would be desired in such a problem, the minimum value justified by the data.

In this method, there is an inaccuracy, usually small, caused by our taking the obtained values of $p_1 \cdots p_k$ for each series as the true values. For, owing to the random sampling occurring within each lot of each series, the obtained values of p for each group of lots (A or B) will have a larger spread (variance) than the true values. This will lead to the variance of the average of these obtained values of p for a given group of lots (and so also to the variance of the average of the differences between the two lots) being somewhat smaller than the variance for the corresponding average of the true values themselves. If then the average difference is found not to be significant in size, in comparison with its error, as above calculated, we may know that, as our calculation is "on the safe side" for this case, our results contain no evidence of a determinate difference. If, on the other hand, a significant difference does seem to be shown, unless it is near the border line of significance there will seldom be need for making a correction for the above source of inaccuracy, for it will be negligible except when both the determinate and the random variation of p from series to series are very great.

The author takes pleasure in acknowledging the valuable advice of Dr. K. Mather, in the making of important revisions during the preparation of the present paper, although Dr. Mather, holding that the case is properly covered by his more general method previously presented,¹ which differs from the method here set forth, is to be held in no way responsible for the latter.

SUMMARY

It is supposed that data on the frequency (p) of events of a given type have been obtained in the form of a number of series ($1 - k$), which may differ determinately from one another, and that each series consists of two lots, representing the contrasting conditions A and B , while the total numbers observed (n) vary irregularly from

¹ K. Mather, *Ann. Eug.*, 6: Part 4: 399-410, 1935.

series to series as well as from lot to lot. Formulae (1, 3) are given for calculating the best weighted average frequencies (\bar{p}) in the two sets of lots, obtained under the two conditions, for the purpose of comparison of the results under the two conditions with one another. The error of the difference between these averages is given (2) and formula (7) is developed for ascertaining the minimum chance of the sets of lots showing as bad a fit as they do to one another, if the difference in conditions *A* and *B* had no real influence on the frequency (p). The purpose of these formulae, then, is to determine to what extent the results indicate that a difference in these conditions influences the frequency.

REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

IN this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of *THE AMERICAN NATURALIST*, in that they deal with the factors of organic evolution. No attempt is made to secure a complete coverage of the pertinent literature, or a uniform treatment. For contributions of major interest, however, interpretive reviews rather than abstracts are favored. During the first year there will be included reviews and notices of selected items which appeared in 1939 and 1940, as well as currently in 1941.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

The Material Basis of Evolution. By RICHARD GOLDSCHMIDT.
New Haven: Yale University Press, 1940: i-xi, 1-436, figs.
1-83. \$5.00.

WHATEVER may be his attitude and his reaction, any biologist who has carefully studied "The Material Basis of Evolution," and who has observed its effect on current biological thought, can hardly deny that this book is an outstanding contribution to the literature of evolution. It is bold, provocative, challenging, at times almost Don Quixotic. The author's wealth of biological experience, his broad comprehension of the literature, his critical inquiring mind, his superior powers of synthesis, his healthy antagonism of the mystical, force the reader first to condone and then almost to forget a too-obvious striving for priority and credit, for a place in the biological sun. Goldschmidt has focused an immense body of evidence on the problem of the mechanics of evolution. Whether championed or opposed, his views demand consideration.

Goldschmidt's treatment is a series of all-or-none contrasts between alternative concepts, of which those on the wrong side are all held to fall together while those on the right side are pictured as the well-matched building stones of a new and more secure biological edifice. The book may therefore be summarized in tabular form:

THE OLD, NEO-DARWINIAN CONCEPTS, TO BE REJECTED

Evolution proceeds through the accumulation of small changes.

Subspecies grade into species, and are incipient species.

Adaptation is a gradual adjustment *in situ*.

Differences on all systematic levels are simply and separately adaptive.

Evolution is gradual; missing links will be found.

There is a common, unified type of evolution: a gradually expanding system.

[Such differences in types of heredity are not recognized.]

Genes are the basis of heredity, and the gradual accumulation of small gene-mutations is the basis of evolution, at all systematic levels. Genes are essentially independent in their action, though interdependence in effects may arise through genic balance.

[These concepts are frequently contrasted with the "classical" or Neo-Darwinian genetics, though the distinctions are not always made clear, except in the comparison of "genic balance" with Goldschmidt's "reaction systems," and of "pattern effect" with "systemic mutation."]

THE NEW, GOLDSCHMIDTIAN CONCEPTS, TO BE ACCEPTED

True evolution results from large, single-step mutations.

Subspecies do not grade into species, and are not incipient species; there are no incipient species.

Preadaptation is the rule.

Subspecific (that is, geographical-race) characters are adaptive to simple environmental factors; specific differentiation involves new and entirely different reaction systems.

Evolution is by large steps; "missing links" never existed.

Evolution is of two distinct sorts: microevolution (within species) and macroevolution (between species and all higher groups).

Alternative inheritance characterizes microevolution; non-alternative heredity holds in macroevolution.

Genes, if they exist at all (which is doubted), can only be involved in microevolution. Through single-step systemic mutations, chromosomal rearrangements (translocations, inversions, multiplication) produce the new reaction systems that comprise macroevolution. Whole chromosomes or even the entire genomes may act as a unit.

Evolutionary changes as well as modifications result from the operation of various factors at different, critical periods of development. The changes have a physiological basis in the quantity and quality of catalysts and hormones, and in the time and rate of their action. Different reaction systems, based on systemic mutations, are involved.

It can not be denied that Goldschmidt has forged a strong chain of biological concepts. I am impressed with the force of each argument, and could muster a large body of speciation data in its support. Many of the points which I made in my contribution to the recent "Symposium on Speciation" harmonize very well with this new evolutionary philosophy. I accept and welcome many of his views, in whole or in part. However, I utterly fail to appreciate the validity of certain of his major premises: (1) that there is a total contrast of evolutionary concepts, as outlined above; (2) that there are two definitely distinct kinds of evolution; (3) that most evolution is by large, complete steps; (4) that genes are non-existent or at least of no major evolutionary significance; and (5) that Neo-Darwinism has been buried.

(1) It strikes me that the more advanced evolutionary thought, as exemplified in "The New Systematics," rightly makes no such distinction as does Goldschmidt between the concepts listed above. In this new thought one does not find a strictly alternative distinction of subspecies *versus* species, of gene-mutations *versus* chromosome-mutations, of genic pattern *versus* reaction systems, of classical genetics *versus* Goldschmidtian genetics or of Neo-Darwinism *versus* modern concepts; nor does one find that all the older conceptions must be sunk to bring into being a new order in biology.

(2) The outstandingly fallacious part of Goldschmidt's evolutionary philosophy, in the reviewer's judgment, is the idea that there are two kinds of evolution, microevolution and macroevolution (or that there is need for these mongrel terms, accepted while "speciation" is rejected as a linguistic atrocity). No student of speciation can rightly deny, now that Goldschmidt has emphasized the point, that a large proportion of subspecies are of no extensive phyletic significance. This is outstandingly true of the many geographical races, whose known differences are almost wholly related to local differences in climate, soil color and the like. But many full species

and genera represent blind alleys too; every line of specialization, minor or major, tends to lead only to its own end.

On the other hand many subspecific differences represent adaptations similar and at times almost identical with those which characterize major evolutionary trends. Thus the differences in body form in general characteristic of the essentially open-water malacopterygian teleosts and the bottom-bound acanthopterygians, or between the swift-swimming scombroid fishes that have secondarily taken to a pelagic existence and their more sluggish ancestors, are approximately matched by the differences in the body form of the subspecies of *Gila robusta*, a minnow that inhabits waters of greatly different current in our western streams. There seems to be nothing consistent or qualitative to distinguish the differences within and between species.

The distinction of microevolution and macroevolution on the basis of different types of heredity, characteristic of intraspecific units and of species, is quite out of agreement with the evidence, at least with that derived from vertebrates. Through an analysis of dozens of naturally produced and experimentally reared hybrids, I have been struck with the complete similarity in the hereditary behavior of all kinds of characters. Ordinary "sports" display a more or less simple type of mendelian inheritance as held by Goldschmidt, but all *systematic* units studied, from minor local races to "good" species and genera, exhibit an apparently blended inheritance. This evidence may or may not be taken to support Goldschmidt's view that "classical" gene-mutations are not involved in speciation, but it goes far to disprove the contention that there are two kinds of evolution.

It would be strange indeed if one kind of evolution were confined to intraspecific differentiation, whereas only one other kind characterized all other systematic levels, from the species to the phylum.

Goldschmidt makes much of the simple environmental

adaptations of subspecies, as contrasted with the different "reaction systems" which he calls species. These reaction systems are described as affecting the animal through and through in physiological as well as anatomical features. Yet the more we study subspecies, the more extensive do we often find to be the differences between populations—and these differences involve various sorts of physiological adaptations as well as structural features. We must conclude that at least many subspecies are "reaction systems" too.

One of the most impressive results of modern taxonomic work—involving experimental and statistical analyses—is that the distinctions between minor races, subspecies, species and genera are very often, and in some groups usually, arbitrary. Decisions as to rank are required, to fit the simple, inflexible nomenclatorial system that is in use, but the more critical systematists can not perceive any fundamental distinction of kind, between subspecies and species. When both phenomena are extensively studied, by observational and experimental evidence, no sharply qualitative difference is found to distinguish racial and subspecific intergradation on the one hand and interspecific and intergeneric hybridization on the other. Hence there is no good evidence of a clear-cut distinction between subspecies and species, or between the types of evolution which need be assumed to explain their origin.

We might conclude that every twig on the tree of evolution does not become a major bough, but that some of the little sprigs, under favorable conditions, do develop into the main branches.

(3) Though the problem is a far more difficult one on which to array evidence, it seems likewise very improbable that evolution ordinarily proceeds by large, complete steps. It is not enough to know that a relatively simple action on some critical stage in development may produce enormous effects on the adult, or to know that the differences between some known terata and the normal indi-

viduals of the species are as great as those separating major groups of animals; nor yet enough to know that a few of these distinctions between the terata and the normal animals closely parallel the group criteria. Genetic potentialities and evolutionary realization may be entirely different.

Most naturalists will be loath to interpret many major mutational changes as possible adaptations or preadaptations. They will find it difficult to conceive of "hopeful monsters" or of any very extensive alterations in structure or function that will not throw the individual entirely out of balance and adjustment with its particular and always complex and intimate environment.

(4) Beyond expressing the thought that there seems to be much good evidence that both gene-mutations and chromosome-mutations are involved in evolution at all levels, I will leave to others a criticism of Goldschmidt's radical views on the very limited effects or complete non-existence of discrete genes.

(5) In his assertedly lethal attack thereon has not Goldschmidt defined Neo-Darwinism as a windmill with which to joust? Does he not overlook the essential Darwinian tenets of lineage and of natural selection? Even if Neo-Darwinism means no more than evolution through the accumulation of small mutations, must the theory be abandoned? Are there not small as well as large mutations? Do not most evolutionary changes arise from at least relatively small mutations (systemic mutations if one wishes)? Is not much of evolution more or less rectilinear, therefore involving a succession of such relatively small mutations? Is Neo-Darwinism transgressed by the fact that some speciation changes have been relatively large and sudden? Is it at all clear that Neo-Darwinism has even been toppled, let alone annihilated by Goldschmidt's sharp lance?

Papers from Tortugas Laboratory, Vol. 32. Carn. Inst. Wash. Publ. 517, 1940 (papers issued separately, 1939-40): i-iv, 1-412, 35 pls., 127 figs. \$4.00 (paper cover), \$4.50 (cloth binding).

IN THIS volume, which maintains the high standard of the series, there are included sixteen reports on biological researches conducted at Tortugas Laboratory. Four of the papers deal with the growth, structure, composition and physiology of the marine alga *Valonia*, and three discuss the systematics, life history and cellulose production of the ascidians of Tortugas. Hugh H. Darby treats a case of abnormal symmetry, and B. R. Coonfield the larval chromatophore system, of a crustacean, *Crangon armillatus*, and Walter N. Hess has a contribution on regional photosensitivity in this species and *Panulirus argus*. William L. and Margot Metcalfe Doyle describe the structure of zooxanthellae and C. M. Yonge and H. M. Nicholas write on symbiosis with these algae, and on the structure and function of the gut, in the mollusc *Tridachnia*. Ciliates from Tortugas are systematically described by W. E. Bullington, and chromatophore reactions in embryos and larvae of a fish, *Pomacentrus leucostictus*, are treated in detail by B. R. Coonfield. Samuel F. Hildebrand, as junior author, has salvaged the results of William H. Longley's years of systematic study on the fishes of Tortugas; some remarkable new genera are described. The last and most extensive paper, by John H. Davis, Jr., deals very interestingly with the ecology and geological rôle of mangroves in Florida. Together these papers constitute a notable contribution to biology.

Heredity and Social Problems. By L. L. BURLINGAME. New York and Boston: McGraw-Hill Book Co., 1940: i-xi, 1-369, figs. 1-77. \$3.50.

PROFESSOR BURLINGAME regards this text-book, and the course of lectures from which it has grown, as a means to accelerate, to mutual and to general advantage, the "growing rapprochement between the biological and the social sciences." I would rather interpret it as an effort to provide, and to apply, a part of that biological foundation without which social science can lay no just claim to partnership in true science. "Heredity and Social Problems" can go far—but not far enough—to teach man

as a social animal to know himself: one of the most fundamental yet most neglected needs not only of a general education, but also, and particularly, of preparation for any of the social professions. The author and Stanford University are to be congratulated for the part they have taken toward the inclusion of the biology of man in college curricula.

Much thought was evidently given to the choice of subject material and to the sequence of its presentation. Factual material was carefully selected for the many tables and graphs. The student's point of view and interests were kept in mind—in places perhaps too obviously. Unfortunately this effort to perfect the book pedagogically has been in part nullified by loose diction. Since the author is an advocate of progressive education, he would hardly justify, as mental calisthenics, a continuous search for hidden antecedents.

Conventional eugenic views are repeatedly stressed. On the basis of human biology there are conservatively discussed possible solutions to varied questions of population, race, mental deficiency, medicine, education (particularly stressed) and government. In general an effort seems to have been made not to shock feelings that are bound up with social, medical and religious convictions.

Social problems are treated from the viewpoint of the present and immediate future. No consideration is given to the possibility that man is undergoing an autogenous, irretrievable degeneration, through the replacement of natural selection by the various and growing provisions of social security (*sensu lato*). In the chapter on heredity and medical problems only one incidental mention is made of what seems to be the biological probability that increasingly effective medical attention is destroying our biological preparedness against the diseases of body and mind. These are social problems that may well transcend our present worries of race and war. Can there be harm in the challenging of our cherished ideas, in the enlargement of our mental vistas?

SHORTER ARTICLES AND DISCUSSION

NEW GENETIC CHARACTERS OF THE TOMATO

THIS is a preliminary report on three new genetic characters of tomatoes found at the Tomato Disease Laboratory of the Texas Agricultural Experiment Station at Jacksonville, Texas. These characters are sticky fruits, yellowish bordered leaves and an unusual double type of fruit. The lists of genetic characters of tomatoes as compiled by Boswell¹ and Crane and Lawrence,² do not include these characters reported here.

The sticky fruited tomato (T328) appeared in 1938 in one plant of *Prairiana* tomato (T158), presumably as a mutation. The *Prairiana* seed was No. 1184B received from Vaughan Seed Store, Chicago, Illinois, in 1938. *Prairiana* is a selection of *Marvana* in Illinois by W. A. Huelsen, who stated in a letter that he had not found tomatoes with sticky fruits. Unlike the *Prairiana* parent, this new plant produces fruits that feel sticky when touched in the mature green-wrap, pink and red stages of maturity. The fruits are soft, and many of them retain numerous glandular hairs. However, the stickiness appears to be partly due to the consistency of the peel. These fruits are regular and a little flat, as their horizontal diameter is nearly one fourth larger than their vertical diameter. They are unusually dark green and become red in ripening. The character of sticky fruits was always associated with abnormally light green leaves and unusually hairy stems. Seed from open-pollinated flowers on the sticky fruited plant was planted in several fields in 1939 and 1940, producing 303 plants, of which 92.4 per cent. bore sticky fruits, while 7.6 per cent. of the plants were like the *Prairiana* parent. This type of segregation can possibly be explained by natural cross pollination with ordinary tomatoes in the fields, although this is an unusually large amount. Plants with sticky fruits were crossed by hand with *Riverside* and *Century* varieties in 1939, and all the artificially crossed flowers were bagged as usual. In 1940, the F_1 progeny of these crosses produced 143 plants, all of which were like their *Century* and *Riverside* parents in lacking the characters of the sticky fruited parent.

¹ V. R. Boswell, "Tomato." U. S. Dept. of Agr. Yearbook of Agriculture, p. 195, 1937.

² M. B. Crane, and W. J. C. Lawrence, "The Genetics of Garden Plants." Macmillan Co., London, 1934.

This is evidence that the associated characters of sticky fruit, light green leaves and very hairy stems are recessive to the ordinary characters of non-sticky ripe fruit on dark green, commonly pubescent plants of the usual commercial types.

Tomato leaves with yellowish-green borders 1 to 4 mm wide characterize Selection T162. These yellowish-green borders are apparent on the young leaves of vigorous plants with maturing fruit. This character often disappears as the plants become senescent. The plants of T162 are like Marglobe in their other characters. Selection T162 originated as a single plant in the third generation from a commercial source of Marglobe tomato seed that had been treated with x-rays. This selection with the yellowish bordered leaves was one of the 134 plants grown by the writer at Jacksonville in 1937. Nearly all the 122 progeny plants of T162, grown in the ensuing three years, showed the characteristic yellowish bordered leaves. This character of yellowish bordered leaves bred true through three generations and presumably is genetic in nature, probably resulting from an x-ray induced mutation. Incidentally, this has the same ancestry as the white-flowered tomato reported previously.³ Selection T162 was crossed artificially with the white-flowered tomato in 1939. The ten F_1 progeny plants from this cross all lacked yellowish borders on their leaves, indicating that this character is recessive. Natural hybridization in the field presumably is the reason why a few of the progeny plants of T162 lacked yellowish borders on their leaves.

Tomato Grande (P. I. 117564) produced two peculiar double type fruits in 1938, while the remainder of the fruits were normal, from 1 to 2 inches long and only 1 inch in diameter. The two abnormal fruits differed in having the lower third of each fruit enlarged as a prominent knob partly separated by a deep constriction. From these two double fruits 11 progeny plants, grown in 1940, produced nearly a tenth of their fruits of this double type.

In addition to these three new genetic characters, evidence has been secured on the genetics of puffing. The Garraprihe (P. I. 117566) variety had most of its fruits extremely puffed. The fruits were dark red, 1 to 2 inches long and 1 inch in diameter, and most of the fruits were hollow like pepper fruits. Both Tomato Grande and Garraprihe are Italian-type varieties purchased from seedsmen in Rio de Janeiro, Brazil. Crosses of

³ P. A. Young, *Jour. Heredity*, 31: 78-79, 1940.

Garraprihe with Marglobe, Riverside and white-flowered tomatoes in 1939 gave an F_1 progeny of 109 plants, all of which had fruits with practically every locule hollow (or extremely puffed). The puff character evidently is dominant in this particular genetic combination. No evidence has yet been obtained as to the number of factors involved.

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POSSIBLE FACTORS CONTROLLING LENGTH OF INCUBATION IN BIRDS

THE difference in length of incubation period of different species of birds has interested many workers. A number of theories have been formulated, but in most of the cases the data available have been so meager that little reliance can be placed on the conclusions.

Bergtold (1917) has compiled from the literature all the published data and added some of his own concerning the length of incubation and possible factors that might control it. From these data he has formulated several theories that should be re-examined in the light of new data.

He first suggests that the optimum incubation temperature for any species is the temperature of the incubating parent. Baldwin and Kendeigh (1932) showed that this theory was incorrect. They found that the average body temperature of the incubating female house wren was 41.3°C ., while the average maximum egg temperature during daylight hours was 37.0°C ., or a difference of 4.3°C . between the average maximum egg temperature and the body temperature of the incubating female. Huggins (in press) found that the average egg temperature for the 11 orders he studied was 34.0°C ., a temperature much below the body temperature of birds.

Bergtold next suggests that a bird's body temperature is closely related to the taxonomic "lowness" or "highness" of the species. Sutherland (1899) had advanced the same idea earlier, drawing his conclusions from body temperatures of birds obtained by use of a clinical thermometer. Simpson (1912) disagreed with Sutherland's conclusions as a result of his own work on Turbinaries, Steganopodes, Pygopodes and Longipennes. Bergtold justifiably points out that there is not enough taxonomic

difference between the birds studied by Simpson to draw such a conclusion.

Bergtold (1917) and Needham (1931) cite Heinroth (1908), who reported that eggs of the Egyptian goose hatch in twenty-eight days under a hen and in thirty days under a Muscovy duck as possible experimental proof that there is a difference in body temperature with "lowness" and "highness" in species. Bergtold further says, "The diminishing size of birds accelerated the metabolic rate, elevated the body temperature, and so shortened the incubation period."

Huggins (in press), in a recent study of egg temperatures in eleven orders and thirty-seven species of birds, has shown that there is probably no significant difference between the average egg temperature in the various orders of birds he studied. He found that the average egg temperature for all birds studied was 34.0° C. with a standard deviation of ± 2.38 . The average egg temperature for the Passeriformes was 33.8° C. Other orders showed no significant difference from this average.

If Sutherland's and Bergtold's theory is true, we should expect to find a significant rise in the egg temperature with a rise in body temperature as we "ascend" the bird orders. Finding a lack of any significant difference in average egg temperatures of the various orders, it is reasonable to suppose that there is little if any difference between the average body temperature of the orders. The smaller birds undoubtedly have a wider range of body temperature than the larger ones, but it is probable that the body temperature under basal metabolic condition would be approximately the same for all birds.

Lastly, Bergtold maintains that the body temperature of the incubating bird is the important factor in the length of incubation. As it has been shown that at least eleven orders of birds have approximately the same egg temperature, therefore there must be other factors that control the length of incubation.

Many suggestions as to the factors involved can be found in the literature. The following are a few: Gurney (1899) suggests that there may be a relationship between longevity and the length of incubation; Gadow (1891) thought that there was a direct relation between length of incubation and the nesting period; Newton (1893) and Evans (1898) suggest that the period of incubation varies, and is related to the state of perfection in which the young are born; Fürbringer (1888), Chapman (1932) and others say that the length of incubation varies roughly with the size of the egg.

Bergtold (1917) and Heinroth (1922) have considered this last suggestion, but came to the conclusion that the correlation between egg weight, species size and length of incubation was too small to be significant.

Huxley (1927) plotted egg size (weight) against body weight of adult on double log paper and found that egg weight varied closely with body weight, although eggs of large birds are not as large as would be expected in proportion. Needham (1931) went a step further and plotted incubation time against egg weight on double log paper, and a definite trend was found showing a general relationship between egg size (weight) and length of incubation.

Worth (1940) plotted egg volume against length of incubation and found in general a positive correlation. Since it is doubtful if many egg weights available represent the weight of freshly laid eggs the use of volume gives a more accurate figure. Using Worth's data the coefficient of correlation was found to be +.643 the standard error $\pm .0578$. This correlation brings out clearly the general relationship between length of incubation and egg volume.

It seems unnecessary to postulate an ecological factor to account for variations in length of incubation compared with egg volume, as Worth does. Errors in the manner of observation and lack of quantitative data would account for considerable variation. For example, Nice (1937), after intensive study, gives the length of incubation for the song sparrow as ranging from a little over 12 days to 15 days.

The evidence presented would seem to indicate that there is a general positive correlation between egg weight or volume and length of incubation. Before the question is clearly settled more data on length of incubation, variations in the length of incubation, fresh egg weights, and hatching weights of birds must be collected.

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DESCRIPTION OF EJACULATORY SAC DIVERTICULA IN CERTAIN DROSOPHILINAE

As far as the author is able to ascertain from a survey of the literature, there is no mention made of the appendage-like diverticula found attached to the ejaculatory sacs of certain members of the subfamily Drosophilinae. Of the thirty-seven species described in the author's unpublished manuscript, eleven had ejaculatory sac diverticula. Nonidez (1920) gives a complete account of the male generative organs of *D. melanogaster*; he discusses in detail the morphology and function of the ejaculatory sac, but since this species does not possess diverticula he has no occasion to describe these structures.

The ejaculatory sac is a pump-like organ which receives the ejaculate from the vas deferens and then forces it into the penis through a short ejaculatory duct. The ejaculatory sac morphology has been described for thirty-six species in the author's unpublished manuscript, but it was found that this structure was absent in an undescribed species of *Gitona*. In working out the comparative morphology of the reproductive tract of thirty-seven species it was noticed that the ejaculatory sac structures differ very considerably among the various species as to size, shape and color. Of particular interest is the fact that the various diverticula group themselves according to four types, and they range in length from short knob-like structures to appendages about eight times the length of the ejaculatory sac itself.

Drosophilinae used in making the dissections were from the genetics laboratory of the University of Texas. Many of these stocks were those developed from wild flies collected in Texas by Dr. J. T. Patterson. Diverticulum studies were made of the following species:

- D. cardini* Sturtevant. 1916.
- D. funebris* Fabricius. 1787.
- D. guttifera* Walker. 1849.
- D. immigrans* Sturtevant. 1921.
- D. macrospina* Stalker and Spencer. 1939.
- D. melanica-like* (undescribed).
- D. nebulosa* Sturtevant. 1916.
- D. putrida* Sturtevant. 1916.
- D. subfunebris* Stalker and Spencer. 1939.
- D. tripunctata* Loew. 1862.
- D. species* (undescribed).
- D. species* (undescribed).
- S. adusta* Loew. 1862.
- S. graminum* Fallén. 1823.

Mature flies, five to ten days of age, were used in making the dissections. Lateral abdominal slits extending to the external genitalia were made with finely ground dissecting needles so that the chitinous material could be teased away. The fatty material, Malpighian tubules and alimentary tract were also removed, leaving the entire reproductive tract free in the physiological saline solution.

The ejaculatory sac diverticula are tubular structures arising from the ventral surface of the sac; they are paired structures and come off from the posterior end; however, in *D. melanica-like* there is an anterior pair of diverticula in addition to the usual posterior pair. In most forms the diverticula appear as continu-

ations of the posterior portion of the sac, and the ejaculatory duct passes through the notch formed between the two appendages. The lumen of the diverticula is continuous with the

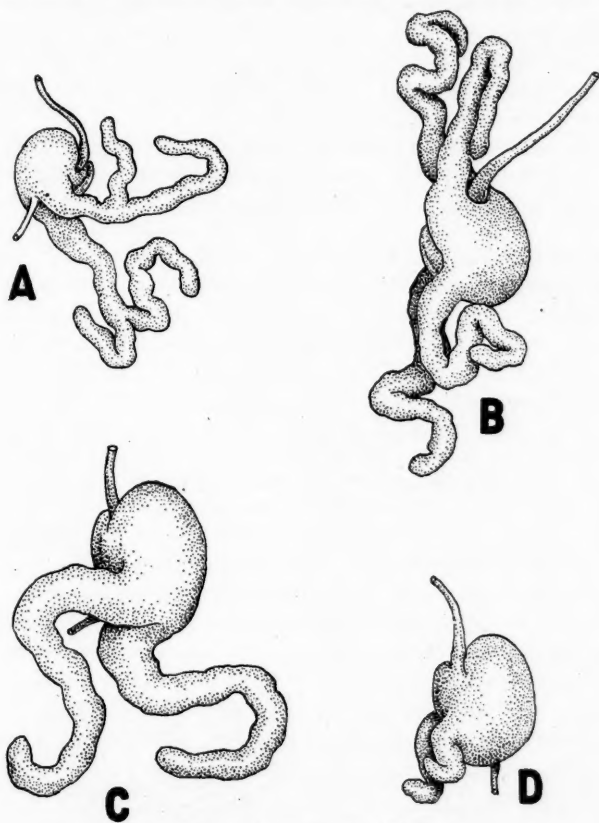


FIG. A. *Scaptomyza adusta*.

FIG. B. *D. melanica*-like (undescribed).

FIG. C. *D. funebris*.

FIG. D. *D. tripunctata*.

cavity of the ejaculatory sac, and it has a blind distal end. The type of cells and the shape of the tubular structures seem to indicate that they are secretory in function. The presence of mucus in the diverticula and their connection with the ejaculatory sac cavity support this view.

The accompanying figures show the four different types of

diverticula found in the subfamily Drosophilinae. Fig. A is a drawing of *Scaptomyza graminum* and represents the forked type of diverticula as found in *S. adusta* and *S. graminum*. In the latter form the diverticula are about three times as long as the ejaculatory sac proper and the branching occurs very near the distal end. In *S. adusta* the diverticula are about eight times as long as the ejaculatory sac and the forking takes place nearer the proximal end.

Fig. B shows the ejaculatory sac of *D. melanica-like*; this is the only species known to have both anterior and posterior diverticula. The appendages are about twice as long as the ejaculatory sac itself.

Fig. C pictures the ejaculatory sac of *D. funebris* and represents the most common type of diverticula as found in *D. cardini*, *D. guttifera*, *D. immigrans*, *D. funebris*, *D. subfunebris*, *D. nebulosa*, *D. macrospina*, *D. species* from Oahu, Hawaii (undescribed), *D. species* from Texas (undescribed) and *D. putrida*. These species are given in order according to the length of their ejaculatory sac diverticula, *D. cardini* having the longest and *D. putrida* having the shortest. The members of this group all have posterior diverticula which fail to branch; the appendages usually coil or form an "s" shaped structure.

Fig. D shows the ejaculatory sac of *D. tripunctata*. This form has two posterior diverticula which are very short, and its ejaculatory sac resembles those of the non-diverticula forms more than the members of any of the other three groups.

In proportion to the size of the ejaculatory sac, the diverticula of *S. adusta* are longer than those of any other species. It was observed that the reproductive tract structures of *D. funebris* were practically identical with those of *D. subfunebris*. It was also noted that there was great similarity between the internal genital apparatus of *D. immigrans* and the undescribed species from Manoa Falls, Oahu, Hawaii; the diverticula in the latter species were slightly shorter than those of *D. immigrans*, but they were of lesser diameter than the appendages of any other species studied.

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